WEST INDIAN XENODONTINE COLUBRID SNAKES: THEIR PROBABLE ORIGIN, PHYLOGENY, AND ZOOGEOGRAPHY

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CONTENTS

ABSTRACT

The relationships between the thirty-three species of xenodontine snakes in the West Indies are reviewed primarily on the basis of osteological and hemipenial morphology. Four species assemblages are recognized, distinguished by the shape of the frontal and prefrontal bones and by the structure of the hemipenis. Within the *cantherigerus* species assemblage three genera are recognized—*Alsophis*, *Hypsirhynchus*, and *Uromacer*. It is suggested that this group entered the West Indies from South or Central America, derived from a primitive form of *Alsophis*. The South American species *Alsophis chamissonis* appears to be a relict of that primitive stock. The mainland genera *Philodryas* and *Conophis* appear to be later specialized descendants from that same early stock. The three Galapagos species formerly referred to the genus *Dromicus* (*biserialis*, *dorsalis*, and *slevini*), are placed in the genus *Alsophis* and regarded as close to the primitive mainland forms. The relationships of the genus *Ialtris* remain uncertain, but descent from West Indian *Alsophis* is reasonable.

The *melanotus* species assemblage has not progressed into the West Indies beyond the northern Lesser Antilles, and has almost certainly been derived from the mainland *Leimadophis-Liophis-Lygophis* complex. The generic name *Dromicus* is applied to these West Indian forms with the name *Leimadophis* as a junior synonym.

Two species, *andreae* and *parvifrons* from Cuba and Hispaniola, respectively, share a number of osteological characters with *Alsophis*, but are like *Dromicus* externally. The hemipenis is of the *Alsophis* type and unlike that of *Dromicus*. Because of their peculiar combination of characters these two species cannot readily be accommodated in any existing genus. The name *Antillophis* nov. gen. is proposed for them. It is suggested that they may be closely related to the mainland form *Lygophis boursieri* while the type species of that genus, *L. lineatus*, appears to be closer to *Dromicus*.

Eight species formerly placed in the genera *Arrhyton*, *Dromicus*, and *Darlingtonia*, are considered to form the *funereus* species assemblage. Except for the retention of *Darlingtonia* for *haetiana*, the species of this group are referred to the genus *Arrhyton*. A close relationship to the mainland genus *Rhadinaea* is postulated, and it is suggested that the two genera may have been derived from a common ancestor. The osteological similarities between these two groups are discussed in terms of general semiburrowing adaptations and are compared with other semiburrowing to burrowing New World colubrid snakes. It is concluded that these similarities represent a phylogenetic relationship rather than morphological convergence.

Four oversea colonizations from the mainland and numerous inter-island dispersals are required to explain the recent West Indian fauna and its present distribution.

INTRODUCTION

The West Indies today contain an endemic snake fauna of modest size. In the absence of an adequate fossil record, any

Fig. 1. Map of the West Indies in Mercator's projection.

discussion of relationships within this group and of its history must ultimately be based on the inferred relationships of living species. It is the purpose of the present study to examine the West Indian species of the subfamily Xenodontinae (sensu Dunn, 1928) of the family Colubridae, with reference to their origin, phylogeny, and zoogeography, so far as these can be deduced from their anatomy and distribution.

The only previous attempt to consider a large segment of this group was that by Dunn, 1932, but his work concerned only the Greater Antilles. Dunn relied heavily on the number of sensory pits present on each of the dorsal body scales and consequently recognized two basic generic groups in the West Indies; Alsophis was distinguished as having two pits per scale, and Dromicus only one pit. From these two groups Dunn derived all of the other endemic genera of the Greater Antilles. He also examined the dentition and hemipenis,

concluding that these did not contradict his proposed relationships. However, examination of Lesser Antillean and mainland species in the present study, as well as a re-evaluation of all West Indian xenodontines, does contradict these conclusions. Dunn weighted his characters in such a way that several well-defined groups of species remained unrecognized.

The xenodontine fauna of the West Indies consists of the thirty-three species and their subspecies listed in Table 1. Tretanorhinus variabilis ssp. occurs on Cuba, and appears to be a recent immigrant from Central America where several closely related species occur; it will not be considered further here. The remaining thirty-two species—except for "Leimadophis" melanotus which occurs both on Trinidad and on the mainland (see Fig. 1 for map)—are endemic to the West Indies and form the basis of this work. All except Ialtris parishi have been examined. They

Table 1

Checklist and distribution of West Indian and some mainland[1] and Galapagos[1] xenodontine colubrid snakes. Generic assignments recognized previous to this paper and recognized in the present study are given for comparison. Species are arranged in alphabetical order.

Species	Generic assignment		Distribution
	Previous	Present	
(*almadensis*)	*Leimadophis*	*Dromicus*	Brazil
andreae andreae	*Dromicus*	*Antillophis* nov. gen.	Cuba
andreae melophyrra			Cuba
andreae nebulatus			Isle of Pines
andreae orientalis			Cuba
andreae peninsulae			Cuba
(*angustilineatus*)	*Dromicus*	*Alsophis*	Peru
anomalus	*Alsophis*	*Alsophis*	Hispaniola
ater	*Alsophis*	*Alsophis*	Jamaica
antillensis antillensis	*Alsophis*	*Alsophis*	Guadeloupe
antillensis antiquae			Antigua
antillensis manselli			Montserrat
antillensis sanctorum			Les Saintes
antillensis sibonius			Dominica
(*biserialis*)	*Dromicus*	*Alsophis*	Galapagos
callilaemus	*Dromicus*	*Arrhyton*	Jamaica
cantherigerus cantherigerus	*Alsophis*	*Alsophis*	Cuba
cantherigerus adspersus			Cuba
cantherigerus brooksi			Swan Island
cantherigerus caymanus			Grand Cayman
cantherigerus fuscicauda			Cayman Brac
cantherigerus pepei			Cuba
cantherigerus ruttyi			Little Cayman
cantherigerus schwartzi			Cuba
catesbyi	*Uromacer*	*Uromacer*	Hispaniola, Tortue Island, Vache Island, Gonave Island
(*chamissonis*)	*Dromicus*	*Alsophis*	Chili, Argentina
cursor	*Dromicus*	*Dromicus*	Martinique
dolichurum	*Arrhyton*	*Arrhyton*	Cuba
dorsalis	*Ialtris*	*Ialtris*	Hispaniola
dorsalis	*Uromacer*	*Uromacer*	Gonave Island
(*dorsalis*)	*Dromicus*	*Alsophis*	Galapagos
exiguus exiguus	*Dromicus*	*Arrhyton*	American Virgin Islands
exiguus stahli			Puerto Rico
exiguus subspadix			Puerto Rico
ferox	*Hypsirhynchus*	*Hypsirhynchus*	Hispaniola
frenatus	*Uromacer*	*Uromacer*	Hispaniola, Beata Island
funereus	*Dromicus*	*Arrhyton*	Jamaica
haetiana haetiana	*Darlingtonia*	*Darlingtonia*	Hispaniola
haetiana perfector			Hispaniola
juliae juliae	*Dromicus*	*Dromicus*	Dominica
juliae copeae			Guadeloupe
juliae mariae			Marie Galante
melanichnus	*Alsophis*	*Alsophis*	Hispaniola
melanotus	*Leimadophis*	*Dromicus*	Trinidad, Tobago, South America
ornatus	*Dromicus*	*Dromicus*	St. Lucia
oxyrhynchus	*Uromacer*	*Uromacer*	Hispaniola
parishi	*Ialtris*	*Ialtris*	Hispaniola
parvifrons parvifrons	*Dromicus*	*Antillophis* nov. gen.	Hispaniola

[1] Non-West Indian species are enclosed in parentheses.

TABLE 1 (Continued)

| Species | Generic assignment | | Distribution |
	Previous	Present	
parvifrons alleni			Gonave Island
parvifrons lincolni			Hispaniola
parvifrons niger			Hispaniola
parvifrons paraniger			Hispaniola
parvifrons protenus			Hispaniola
parvifrons rosamonde			Vache Island
parvifrons stygius			Hispaniola
parvifrons tortugensis			Tortue Island
perfuscus	*Leimadophis*	*Dromicus*	Barbados
polylepis	*Dromicus*	*Arrhyton*	Jamaica
portoricensis portoricensis	*Alsophis*	*Alsophis*	Puerto Rico
portoricensis anegadae			Anegadae
portoricensis aphantus			Vieques
portoricensis nicholsi			Buck Island
portoricensis prymnus			Puerto Rico
portoricensis richardi			St. Thomas
portoricensis variegatus			Mona Island
rijgersmai	*Alsophis*	*Alsophis*	Anguilla Bank Islands
rufiventris	*Alsophis*	*Alsophis*	St. Kitts, Saba, St. Eustatius, Nevis
sancticrucis	*Alsophis*	*Alsophis*	St. Croix
(*slevini*)	*Dromicus*	*Alsophis*	Galapagos
(*tachymenoides*)	*Dromicus*	*Alsophis*	Peru
taeniatum	*Arrhyton*	*Arrhyton*	Cuba
variabilis	*Tretanorhinus*	(not considered)	Cuba
vittatum vittatum	*Arrhyton*	*Arrhyton*	Cuba
vittatum landoi			Cuba
vudii vudii	*Alsophis*	*Alsophis*	Great Bahama Bank Islands
vudii alterrinus			Grand Bahama Island
vudii picticeps			Bimini Island
vudii raineyi			Crooked Island
vudii utowanae			Great Inagua Island

are divided into four species assemblages on the basis of skull, hemipenial, and external characters, and will be treated within these groups in the following pages. All described subspecies except "*Dromicus*" *andreae peninsulae* and "*D.*" *a. melophyrrha* from Cuba, "*Dromicus*" *juliae copeae* from Guadeloupe, and "*D.*" *exiguus subspadix* from Puerto Rico, have been examined; but subspecies will not be discussed further unless the evidence suggests a change in taxonomic rank. The osteology of 70 main-

land and Galapagos species was examined in order to determine possible relationships between Antillean and mainland forms.

Some previous generic allocations are here considered to be of questionable validity. I, therefore, as an initial procedure, will disregard current generic assignments and use only the specific names until probable relationships have been assessed and assemblages of probable generic value can be recognized. Changes in nomenclature are made only where
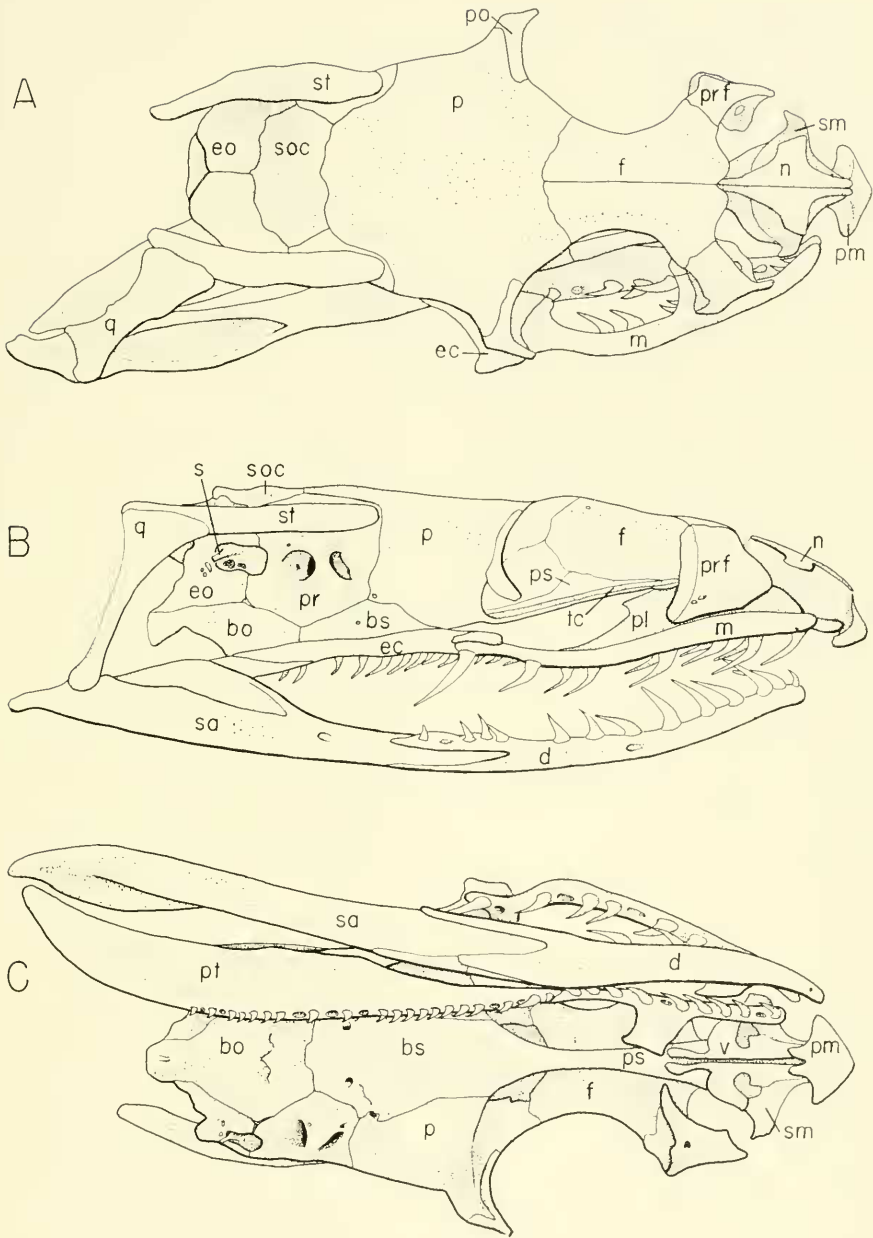
Fig. 2. Skull of *Alsophis cantherigerus* (MCZ 44874) showing general relationships of bones in xenodontine colubrid snakes. A, dorsal view; B, lateral view; C, ventral view. Left tooth-bearing elements removed. Abbreviations: *bo*, basioccipital; *bs*, basisphenoid; *d*, dentary; *ec*, ectopterygoid; *eo*, exoccipital; *f*, frontal; *m*, maxilla; *n*, nasal; *p*, parietal; *pl*, palatine; *pm*, premaxilla; *po*, postorbital; *pr*, prootic; *prf*, prefrontal; *ps*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *s*, stapes; *sa*, surangular; *sm*, septomaxilla; *soc*, suprooccipital; *st*, supratemporal; *tc*, trabecular canal; *v*, vomer. Approx. × 7.

necessary for consistency and for the logical implementation of generic concepts as developed here. In a final section I use the postulated relationships to suggest a possible interpretation of the zoogeographic history of what I consider to be the valid groups in the West Indies.

It is my feeling that snake genera are oversplit and not comparable to genera in other reptilian groups. This is a subjective judgment, however, and certainly not consistent with the philosophy and usage of the majority of herpetologists working on snakes. Since it is certainly desirable that taxonomic usage within the West Indies conform to that customary elsewhere, I have conservatively retained generic names (e.g., *Darlingtonia*) though I believe them to be of limited usefulness. In one case I have raised to generic rank a species group which, on current taxonomic usage, cannot be accommodated within any other existing genus.

As Darlington (1938) and Simpson (1956) have discussed, the islands of the Caribbean do not appear to have been connected with the mainland during the later Cenozoic and overseas migration best explains the available faunal evidence. This hypothesis seems best also to explain the present data.
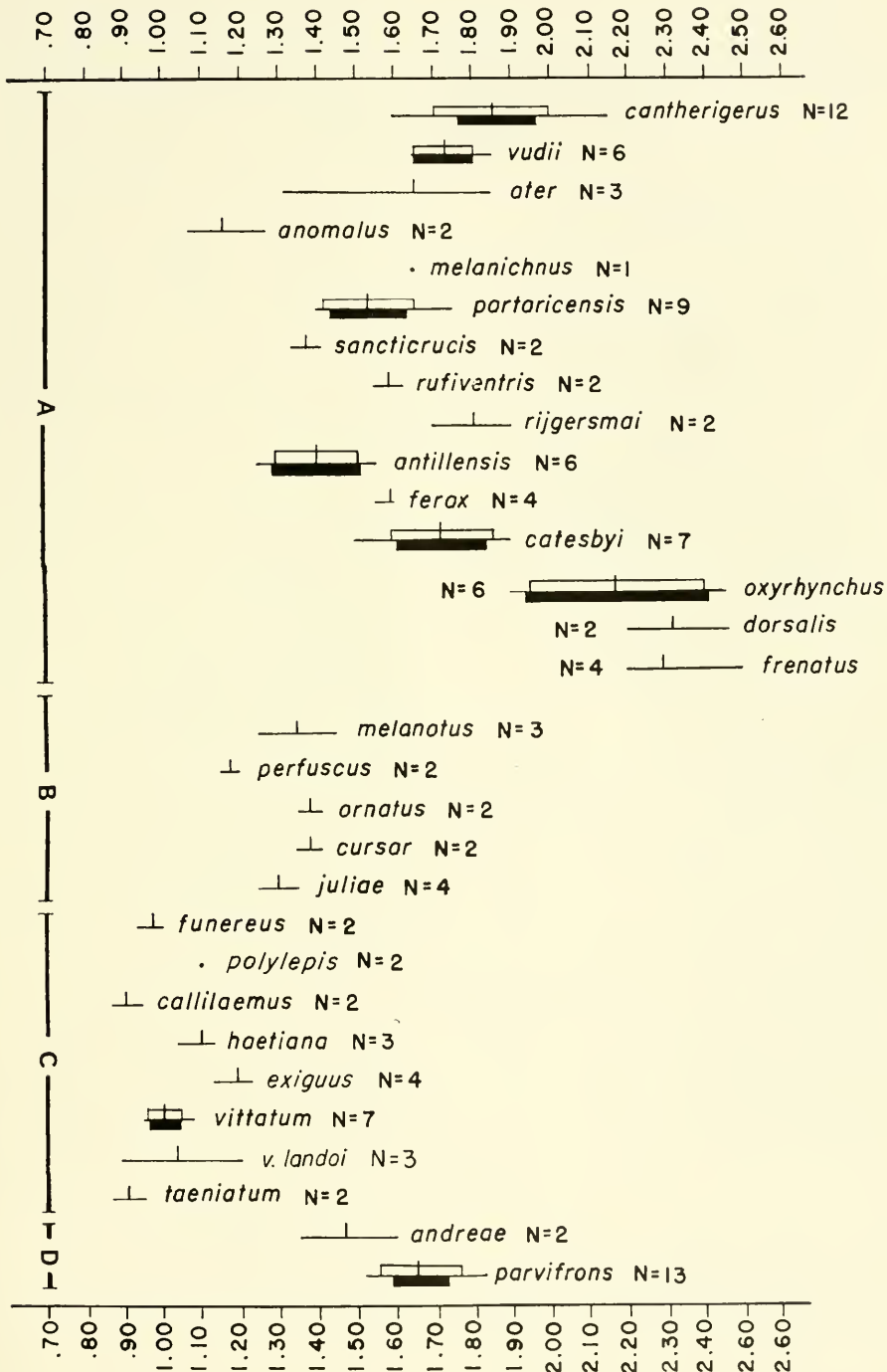
Characters utilized

The choice of specific skull characters was made only after more than 200 skulls of West Indian and mainland species had been examined to determine which characters were least variable within a species and to discover which ones could therefore be used to infer possible relationships with other species. The characters so chosen include the following:

1. The number of teeth which, in several of the species assemblages recognized here, show trends of reduction or increase from species to species (see Figs. 6, 20, and 29 below and the appendix).

2. The frontal bones (see Fig. 2 for labeled skull) also show considerable variation in shape within the West Indies, but prove to have distinctive proportions in certain assemblages, long and narrow on one group and nearly square in another. Figure 3 shows the distribution of length/width ratios for the frontal bones in 29 West Indian species. The four groups of species labeled A, B, C, and D represent the species assemblages recognized here on the basis of all characters combined. Nevertheless, even with respect to frontal shape alone, it is clear that assemblage C may be distinguished from assemblages A and D in having a frontal pair that is roughly as wide as it is long. In assemblage A, most of the species have a frontal pair that is one and one-half to two times as long as wide.

3. The shape of the prefrontal bone was found to be very reliable in separating assemblages in most cases, but quantification of this character was difficult. In Figure 4 the same 29 species as in Figure 3 are compared with respect to the length/width index for the prefrontal bone. Although assemblages B and C overlap completely, both exhibit a considerably longer and narrower prefrontal than in assemblage A (Fig. 5). Although there is a certain degree of variation with respect to shape of the prefrontal and other bones, they remain sufficiently distinctive in each group to be taxonomically useful. Other characters such as the parasphenoid width and skull proportions are discussed under each species assemblage.

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Fig. 3.   Length/width indices for the frontal bone pair of 29 species of West Indian colubrid snakes. A, *cantherigerus* species assemblage; B, *melanotus* species assemblage; C, *funereus* species assemblage; D, *andreae* species assemblage. Horizontal line, observed range; vertical line, mean; open rectangle, ± one standard deviation from the mean; solid rectangle, 95 per cent confidence interval of the mean.
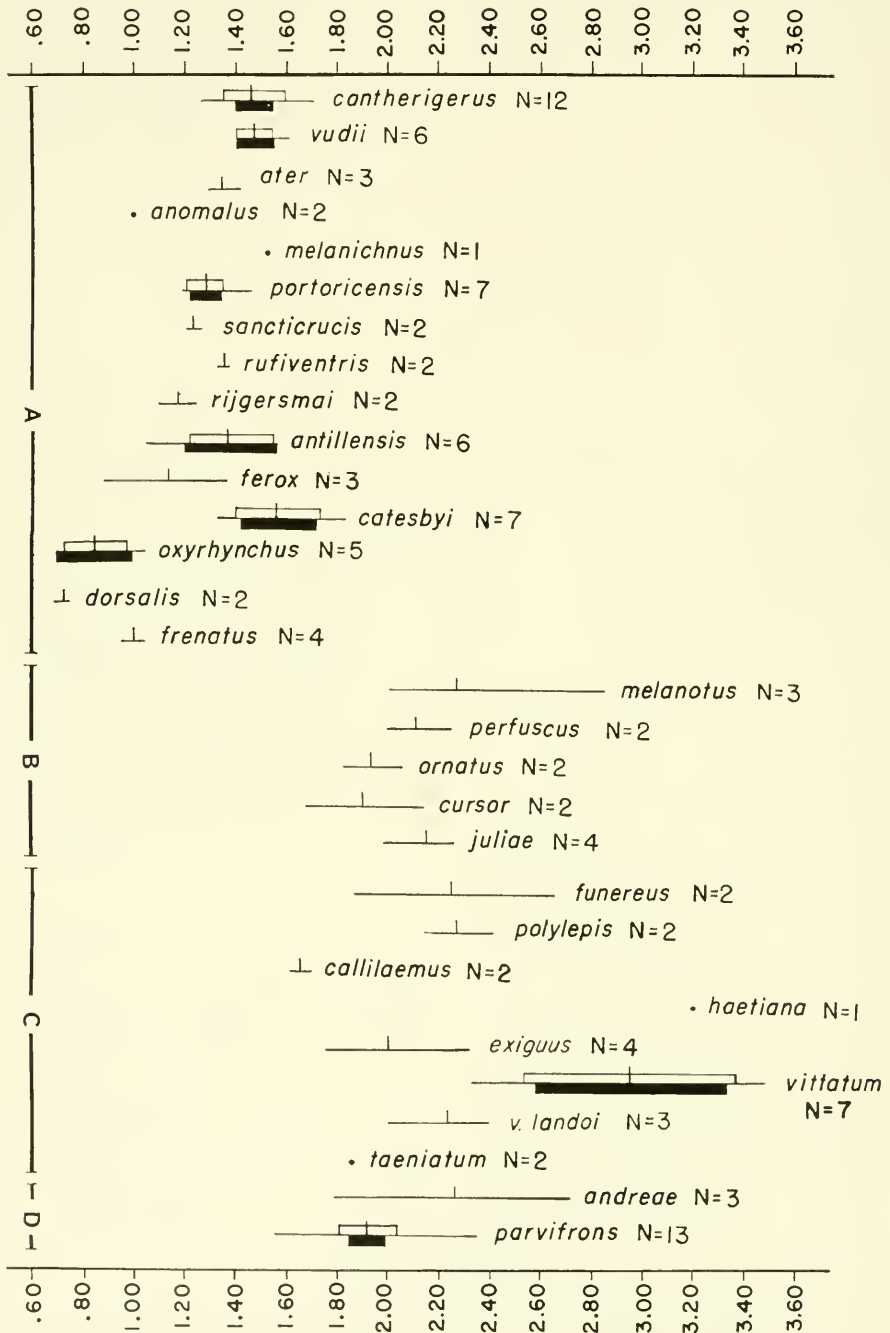
.70 .80 .90 1.00 1.10 1.20 1.30 1.40 1.50 1.60 1.70 1.80 1.90 2.00 2.10 2.20 2.30 2.40 2.50 2.60

A

cantherigerus N=12

vudii N=6

ater N=3

anomalus N=2

· melanichnus N=1

portoricensis N=9

sancticrucis N=2

rufiventris N=2

rijgersmai N=2

antillensis N=6

ferox N=4

catesbyi N=7

N=6　oxyrhynchus

N=2　dorsalis

N=4　frenatus

B

melanotus N=3

perfuscus N=2

ornatus N=2

cursor N=2

juliae N=4

C

funereus N=2

· polylepis N=2

callilaemus N=2

haetiana N=3

exiguus N=4

vittatum N=7

v. landoi N=3

taeniatum N=2

D

andreae N=2

parvifrons N=13

.70 .80 .90 1.00 1.10 1.20 1.30 1.40 1.50 1.60 1.70 1.80 1.90 2.00 2.10 2.20 2.30 2.40 2.60 2.60

Fig. 4.   Length/width indices for the prefrontal bone of 29 species of West Indian colubrid snakes.   Symbols as in Fig. 3.

The discussions of hemipenial morphology are based on dissections *in situ* of the uneverted organ. Terminology is after Dowling and Savage (1960).

It must be emphasized that in this study most measured parameters show various degrees of overlap in range for various species. This does not, however, lessen their value in attempting to recognize phylogenetic relationships through an analysis of morphological similarities. If an insular series of closely related species has been successively derived by island-hopping in a linear sequence, we might expect any two adjacent forms to show a greater similarity, barring extreme specialization, than the two geographically terminal species of the series.

The characters used here are those that combine relatively little intraspecific variability and enough variation between species to be useful in the study of intrageneric relationships. Certain characters such as an apical awn on the hemipenis, the shape of the prefrontal bone, or certain skull proportions appear to be constant within groups of species that show a close relationship in totality of characters combined, and are therefore considered to be of maximum value in indicating true affinities. Others, such as the number of pits on each dorsal body scale, have sometimes proved inconsistent with the majority of other traits and have therefore been considered unreliable at the level of major groups.

AGE VERSUS HABITUS

When attempting to establish relationships between extant forms based entirely on morphological considerations, it must be reasonably certain that differences are not the result of allometric phenomena. Likewise, it must be reasonably clear that apparent similarities are not the result of habitus rather than a close phylogenetic relationship.

Juvenile specimens, when available for comparison with the corresponding adult forms, show a number of consistent differences in the structure of the skull which appear to be related solely to size. The major differences may be summarized as follows:

Juvenile skull

Skull relatively wide
Quadrate thin and triangular
Supratemporal relatively short
Crests low and rounded
Postorbital small, non-projecting
Orbital foramen very large
Pterygoids short, not projecting beyond
 foramen magnum
Maxilla relatively lightly built
Bones of brain case thin

Adult skull

Skull relatively narrow
Quadrate with rodlike shaft
Supratemporal relatively long
Crests high and sharp
Postorbital large, projecting
Orbital foramen small
Pterygoids long, projecting far beyond
 foramen magnum
Maxilla relatively massive
Bones of brain case thick

It is clear that these characters should not ordinarily be given high taxonomic weight unless the comparison is between two species of comparable adult size.

Similarities resulting from habitus adaptations are more difficult to establish because the mode of life of these species is so poorly understood, and also because the adaptive significance of certain characters, such as scale pits, is at present unknown. Character convergence resulting from habitus similarity can, however, be inferred if a large number of characters are studied together. This point will be discussed in greater detail under the *funereus* species assemblage below.

THE SPECIES ASSEMBLAGES

Four species assemblages have been distinguished among the 32 species of West Indian xenodontine snakes here under study. These are characterized on the basis of a number of traits as follows:

	Prefrontal	Frontals	Hemipenis	Size
cantherigerus assemblage	long anteroposteriorly	long and narrow	no disk	large
melanotus assemblage	short anteroposteriorly	short and narrow	apical disk	medium
andreae assemblage	short anteroposteriorly	long and narrow	no disk	medium
funereus assemblage	short anteroposteriorly	square	no disk	small

CANTHERIGERUS SPECIES ASSEMBLAGE

Included West Indian species: *anomalus* PETERS, Hispaniola; *antillensis* (= *leucomelas*)[1] SCHLEGEL, Antigua, Montserrat, Guadeloupe, Les Saintes, Dominica; *ater* GOSSE, Jamaica; *cantherigerus*[2] BIBRON, Cuba, Isle of Pines, Swan Island, Grand Cayman, Little Cayman, Cayman Brac; *catesbyi* SCHLEGEL, Hispaniola, Tortue Island, Vache Island, Gonave; *dorsalis* DUNN, Gonave; *ferox* GÜNTHER, Hispaniola; *frenatus* GÜNTHER, Hispaniola; *melanichnus* COPE, Hispaniola; *oxyrhynchus* DUMÉRIL AND BIBRON, Hispaniola; *portoricensis* REINHARDT AND LÜTKEN, Puerto Rico, Mona Island, Virgin Islands; *rijgersmai* COPE, Anguilla Bank Islands; *rufiventris* DUMÉRIL AND BIBRON, Saba, St. Eustatius, St. Kitts, Nevis; *sancticrucis* COPE, St. Croix; *vudii* COPE, Great Bahama Bank Islands, Great Inagua.

Osteology. The present group of species may be distinguished from other West Indian xenodontines by a number of skull features, the most characteristic of which is the shape of the prefrontal bone (see Fig. 5). Here this element is wide anteroposteriorly with a broad and strongly convex anterior edge. The lower margin of this anterior edge curves medially above the lacrimal foramen, so that the latter opens anteroventrally.

Within the assemblage, the species *cantherigerus* (Cuba) has the lowest number of teeth, with an average dental formula of about $12 + 2$ maxillary, 10 palatine, 26 pterygoid, and 19 dentary teeth (see Fig. 6 and the Appendix for variation). The skull (Fig. 7) is long and the cranium is moderately deep dorsoventrally. The frontals are widest anteriorly where they make contact with the prefrontals and are strongly emarginated above the orbits. A short, stout postorbital bone is articulated in a deep notch on the parietal bone in such a way that a prominent flange or lateral extension of the parietal intervenes between the postorbital and the frontal bones (see Fig. 2). A weak, but clearly visible groove marks the dorsal midsagittal line of the parietal bone. The parasphenoid, forming the midventral surface of the skull, is narrow and has a deep trabecular canal on each lateral surface. This groove extends from the orbital foramen to the nasal capsule. A dorsal extension of the parasphenoid bone above the trabecular canals separates the two orbits, forming a thin interorbital partition.[1] The supratemporal is strong and curved, and extends some distance beyond the occiput. The quadrate is long and straight.

The species *vudii* on the islands of the Great Bahama Bank does not significantly differ osteologically from *cantherigerus*. The dental formula is about $12 + 2$ maxillary, 10 palatine, 24 pterygoid, and 21 dentary teeth for *vudii vudii* and is roughly comparable to that of *cantherigerus*. A peculiar feature of *vudii* is the melanic

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[1] As discussed by Schwartz (1966: 178), Brongersma's (1937) analysis of Schlegel's cotypes and his choice of the Guadaloupe-like specimens as the lectotype of *Alsophis antillensis* have reduced the name *leucomelas* to the junior synonymy of *antillensis*.

[2] Senior synonym of *angulifer;* see Smith and Grant, 1958.
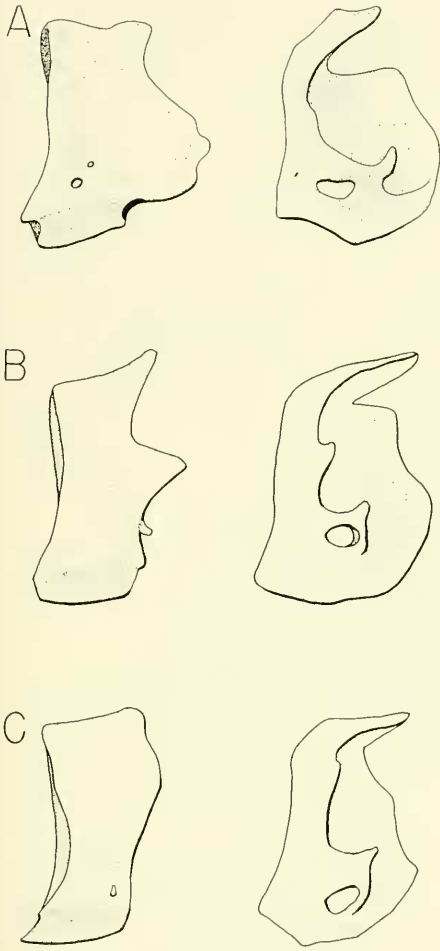
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[1] Equals frontal crests of Underwood, 1967.

Fig. 5. Comparison of the three prefrontal bone types found in the four species assemblages of West Indian colubrid snakes as discussed in the text. A, *cantherigerus* assemblage type (*Alsophis cantherigerus*, MCZ 11200); B, *melanatus* and *andreae* assemblage type (*Antillophis parvifrons*, nav. gen., MCZ 77227); C, *funereus* assemblage type (*Arrhyton polylepis*, MCZ 81020). For each: left, lateral view; right, anterior view. Not to scale. Approx. × 10.

tissue lining the cranial cavity of every specimen examined. This tissue imparts a bluish gray color to the skull. A similar condition occurs occasionally in *cantherigerus*, and also in *catesbyi*, *dorsalis*, *frenatus*, and *oxyrhynchus* where it is the usual condition.

Although only two specimens including the type were available for study, *vudii utowanae* from Great Inagua differs from all the subspecies of *vudii* on the Great Bahama Bank in several characters. The nasal bone is distinctive in shape, but this character appears to be somewhat more variable than most skull characters and is therefore of uncertain significance. In its dentition, however, *vudii utowanae* is quite distinct from the other subspecies. The dental formula is about $15 + 2$ maxillary, 13 palatine, 30 pterygoid, and 23 dentary teeth, and is greater for every tooth-bearing element. When additional specimens of *utowanae* become available, a greater degree of overlap with the Bahama Bank forms may become evident. However, *utowanae* still will largely lie outside the neatly clustered range for the other subspecies of *vudii*. As in *vudii vudii*, the skull of *utowanae* appears bluish gray due to the melanic tissue lining the cranial cavity.

On Jamaica the species *ater* has a dental formula higher than that of *cantherigerus*. The skull is generally flatter (Fig. 8) and, as a result of this flattening, the nasal bones are closer to the septomaxilla, and the frontal bones touch the trabecular canals ventrally so that the interorbital partition is very small, consisting only of that portion of the parasphenoid bearing the trabecular canals. The frontal bones are relatively shorter and wider (Fig. 9) in contrast to the long, narrow frontals of the Cuban species. In all other skull characters the two forms are very similar. The septomaxillae are expanded anteriorly and widen immediately behind the premaxilla (Fig. 10B).

The name *capistrata*, introduced by Gosse (1851: 373) for a patterned form from Jamaica, was synonymized with *ater* by Boulenger (1894) without comment. Two specimens of this form from the British Museum were made available to me for comparative purposes. Both are smaller than typical *ater* and differ from it in a number of osteological characters which in other species are related to

MAXILLARY TEETH

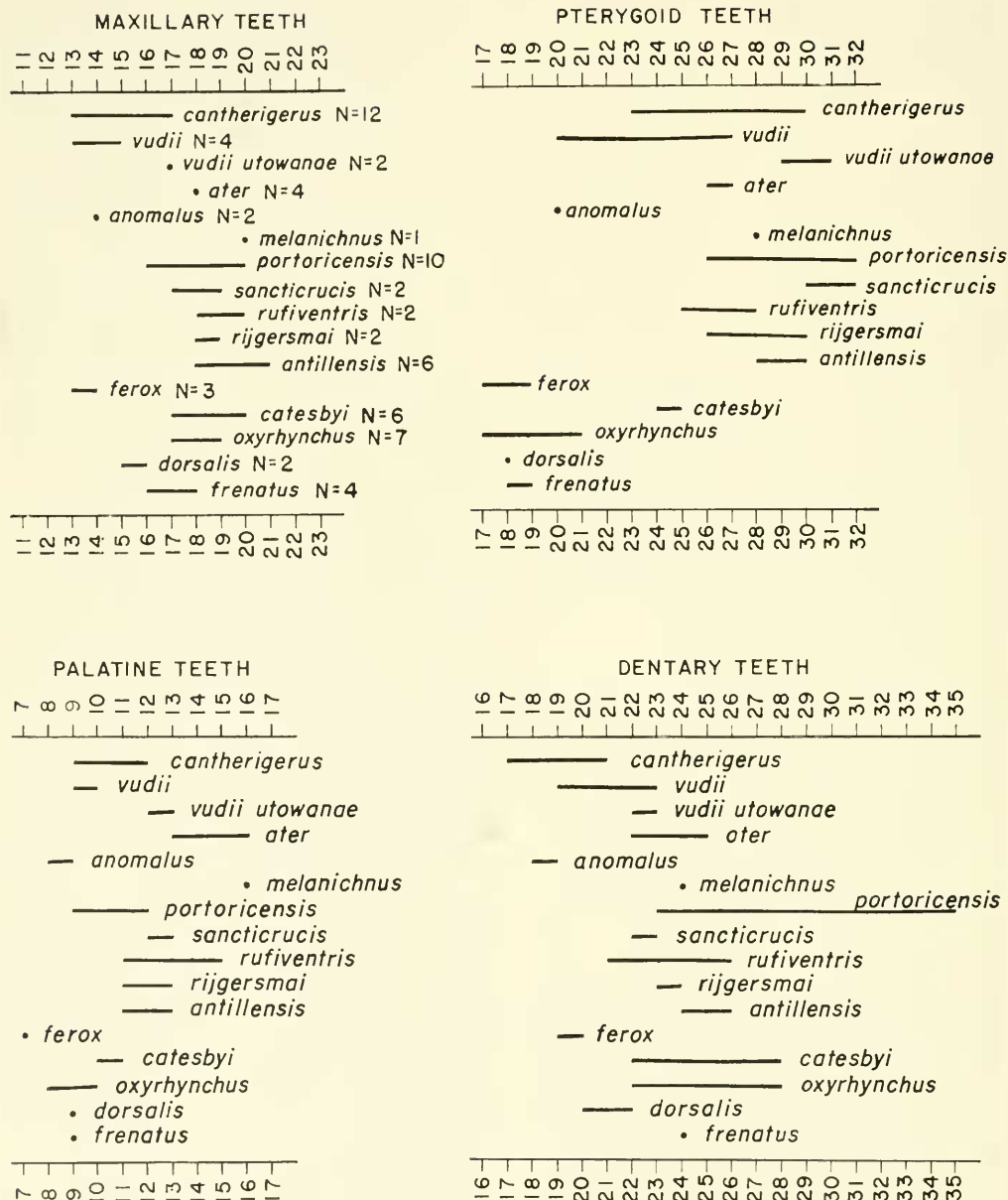PTERYGOID TEETH

PALATINE TEETH

DENTARY TEETH

Fig. 6. Observed ranges of variation in numbers of teeth on each tooth-bearing element for the 15 West Indian species of the *cantherigerus* species assemblage.

ontogenetic changes. These include relatively narrower frontals, a broad rounded cranium, low crests and ridges, and thin cranial bones. It thus seems likely that *capistrata* represents a juvenile stage of *ater*, and we may follow Boulenger in regarding the two as synonymous.

On Hispaniola there are eight species
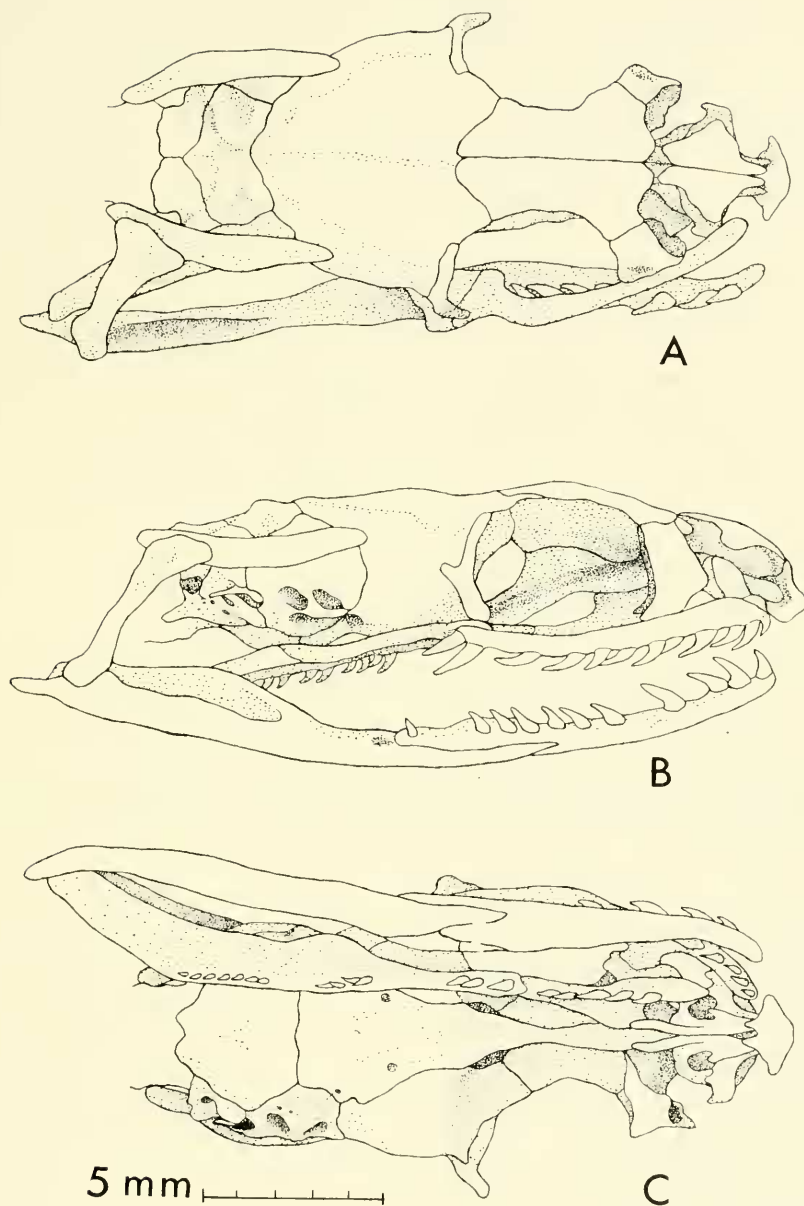
Fig. 7.   Skull structure of *Alsaphis cantherigerus*, MCZ 56429.   A, dorsal view; B, lateral view; C, ventral view.

that may be placed in the present species assemblage. In the rare form *melanichnus*, the numbers of teeth are higher than in either *cantherigerus* or *ater*; the dental formula is 18 + 2 maxillary, 16 palatine, 28 pterygoid, and 24 dentary teeth. The posterior processes of the vomer are laterally expanded into flat plates, oval in shape when viewed from below. This character is not seen in any other West Indian
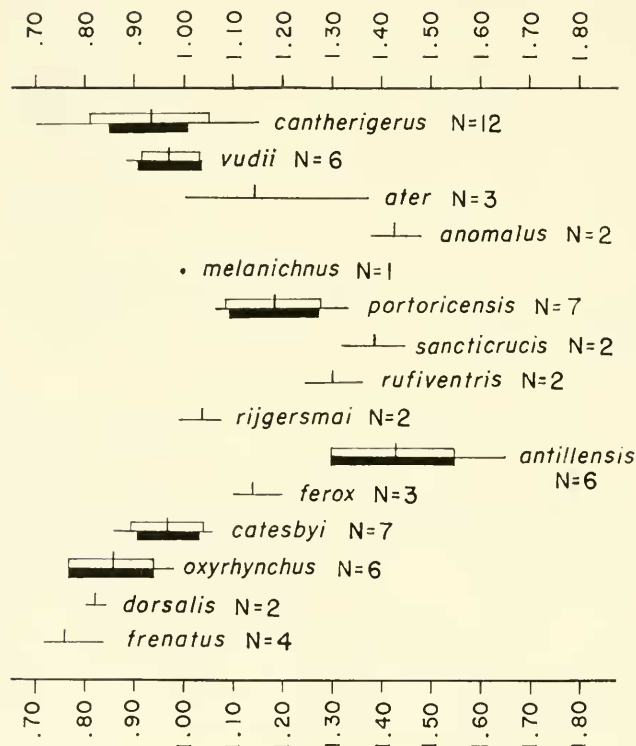
Fig. 8. Frontal bone width/preorbital skull depth indices for the 15 West Indian species of the *cantherigerus* species assemblage. Horizontal line, observed range; vertical line, mean; open rectangle, ± one standard deviation from the mean; solid rectangle, 95 per cent confidence interval of the mean.

xenodontine. In comparison to *cantheri-gerus*, the postorbital bone is wider in proportion to its length, and the frontal is relatively slightly shorter. The supra-temporal is short and stout.

Another Hispaniolan species, *anomalus*, is closer in many ways to *cantherigerus* (Cuba) than it is to *melanichnus*, espe-cially in the structure of the vomer, post-orbital, and supratemporal. The skull is proportionately slightly wider and more dorsoventrally depressed, anterior to the orbit, than in the Cuban form. The pre-maxilla is a solid, heavy structure, semi-circular in ventral view, and quite unlike that of other members of the assemblage. Ventrally, the parasphenoid is wider be-neath the orbits than in *cantherigerus* and forms only a short interorbital partition

(Fig. 11). The skull has numerous high crests and ridges for muscle attachment, but these crests appear to develop with positive allometry in most large speci-mens of xenodontines and are almost certainly related to the great size of this species. In its dentition, *anomalus* shows only slight modifications from the con-dition found in *cantherigerus* (Cuba), and has a formula of about 12 +2 maxil-lary, 8 palatine, 20 pterygoid, and 19 dentary teeth.

Also found on Hispaniola is the well-defined species *ferox*. (I include speci-mens from the southwest peninsula of Haiti which consistently lack a loreal scale.) This form is remarkably like *ater* (Jamaica) in dorsoventral flattening of the skull, in the short, wide frontal, and
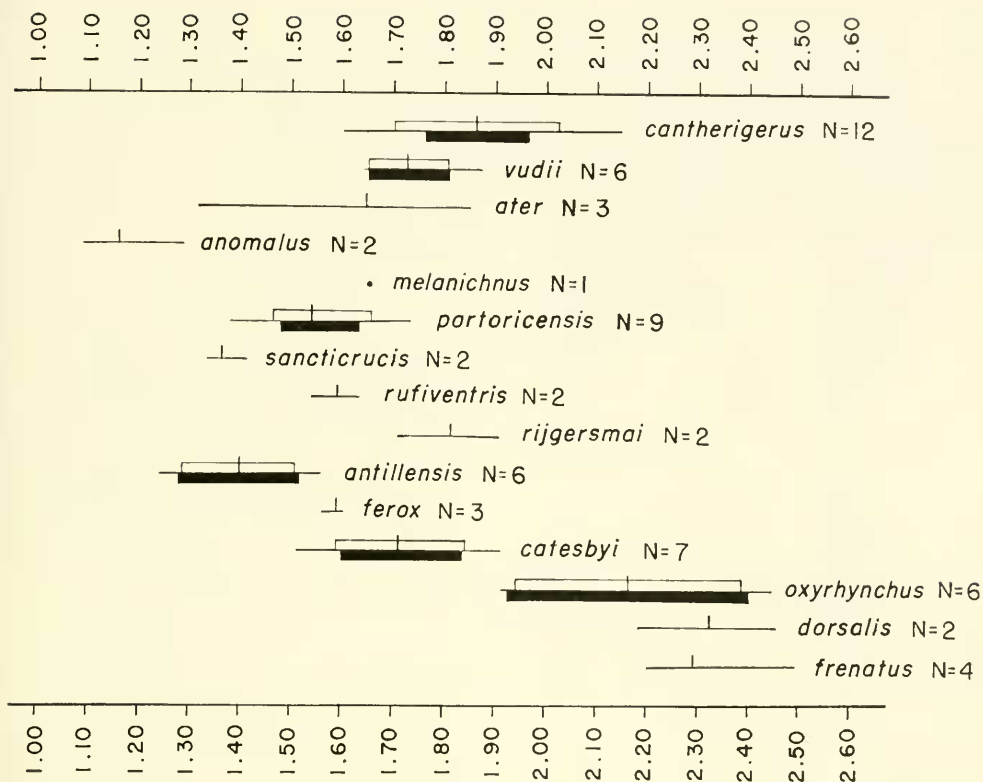
Fig. 9. Length/width indices for the frontal bone pair of the 15 West Indian species of the *cantherigerus* species assemblage. Symbols as in Fig. 8.

in the very small parasphenoid inter-orbital partition. The septomaxilla is even more expanded than in the Jamaica species (Fig. 10C), and the nasal area is depressed dorsoventrally as in that species so that the nasal bones lie close to the septomaxilla. In all of these characters this species is suggestive of *catesbyi* (discussed below). In its dental formula *ferox* shows a reduction in the number of teeth, as compared with *ater*. The teeth of *ferox* are larger than in *ater*, but this character is somewhat variable in specimens of equal size. In all other characters the similarity between *ferox* and *ater* is striking. The only notable osteological difference is in the shape of the nasal (Fig. 12), which in *ferox* is wide anteriorly and tapers off behind.

The four remaining Hispaniolan species are clearly united into a single sub-assemblage on the basis of external morphology (see below). Within the sub-assemblage, *catesbyi* is the least specialized and is very similar to *ferox* in skull structure; few cranial characters can adequately separate the two species. The major difference is in the higher dental formula in *catesbyi*. The teeth are enlarged as compared with *ater*, but not as much as in *ferox*, except for the palatine and pterygoid teeth which are as large as in that species. The most notable similarities between *ferox* and *catesbyi* are in the anteriorly expanded septomaxilla (Fig. 10), and in the dorsoventrally depressed preorbital portion of the skull. The nasal of *catesbyi*, although distinct in
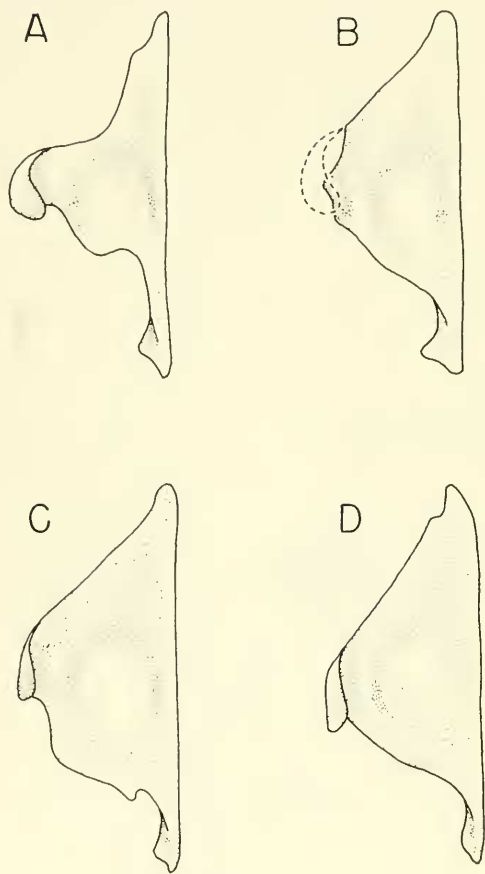
Fig. 10. Left septomoxillo of four species of the can-therigerus species ossembloge. Dorsal view. A, *Alsophis cantherigerus*, MCZ 8611; B, *A. ater*, MCZ 6005; C, *Hypsirhynchus ferox*, MCZ 64785; D, *Uromacer catesbyi*, MCZ 3605. Not to scale. Approx. × 5.

shape, is not very different from that of *ferox*. The more highly specialized species of this subassemblage, *oxyrhynchus*, *dorsalis*, and *frenatus*, have greatly elongated nasals, vomers, and septomaxillae. The dentary, maxilla, and palatine are also elongated, thus extending the dental row forward. The species *oxyrhynchus* and *dorsalis* are the most highly specialized forms with an exaggeration of all these characters.

On Puerto Rico and the Virgin Islands the species *portoricensis* occurs. In the structure of its nasal, premaxilla, supratemporal, and quadrate (Fig. 13), it is more like *cantherigerus* (Cuba) and *anomalus* (Hispaniola) than like *melanichnus* (Hispaniola). The interorbital partition is small and the frontal is shorter antero-posteriorly than in the Cuban species. Ventrally the parasphenoid is wider than in either *cantherigerus* or *melanichnus*. The dental formula is higher than in *cantherigerus*, but there are fewer maxillary and palatine teeth than in *melanichnus*. The subspecies *portoricensis nicholsi* and *p. anegadae*, both from the Virgin Islands, are similar to each other in having a longer and narrower frontal bone than other subspecies of *portoricensis*. In *p. anegadae* the parasphenoid is very narrow, but in *p. nicholsi* this bone is as wide as in other subspecies of *portoricensis*.

On the northern islands of the Lesser Antilles there are four species that are osteologically very close to *portoricensis*. Most similar is *sancticrucis* from St. Croix which is osteologically inseparable from that species. On Saba, St. Kitts, St. Eustatius, and Nevis, the species *rufiventris* is also very close to the Puerto Rican species in most osteological characters. The form on St. Barthelemy and Anguilla, *rijgersmai*, is another member of what may be called the *portoricensis* species group. In most characters of the skull and in the dentition, this form is like the Puerto Rican species. The nasal is like that of *rufiventris*, but the skull is narrower throughout, and the premaxilla reduced in size. The frontal is proportionately narrower than in other members of this subgroup. One other member of the group is *antillensis* (= *leucomelas*) which in most characters of skull morphology is like *rufiventris* (St. Kitts, etc.). Unlike *rijgersmai* the frontal is broad and the premaxilla is unreduced. The dentition in all of these species of the *portoricensis* species group is similar when the degree of variation in each is taken into account (see Fig. 6).
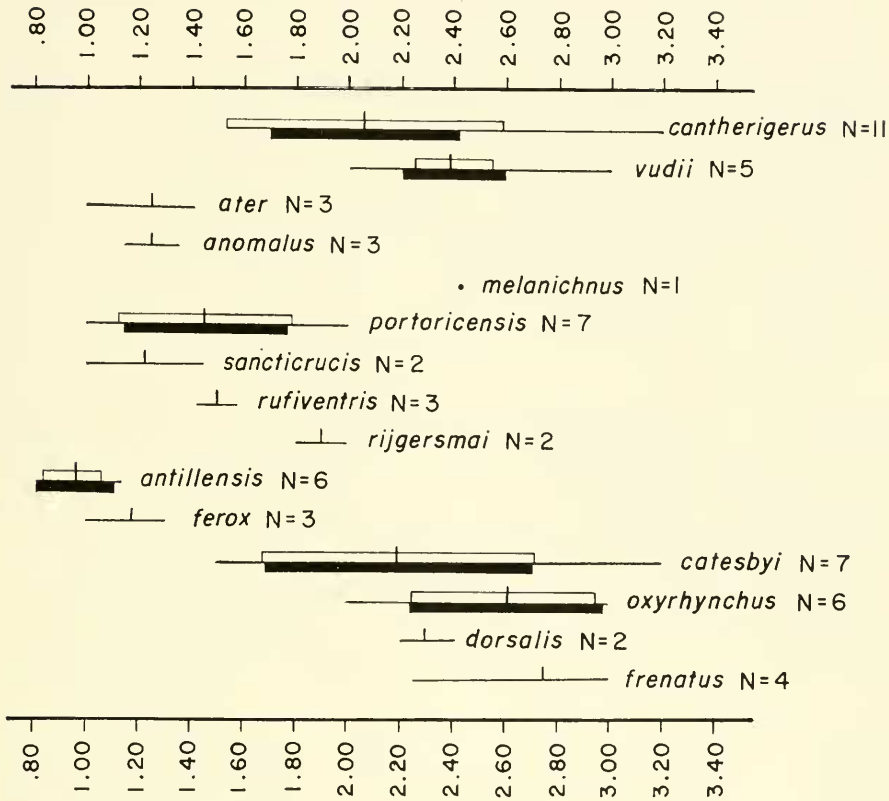
The species of the *portoricensis* species

Fig. 11. Interorbital height/ventral width indices for the parasphenoid bone of the 15 West Indian species of the *cantherigerus* species assemblage. Symbols as in Fig. 8.

group show a far closer relationship among themselves than they do to any other species in the *cantherigerus* assemblage, although they are clearly part of that assemblage. The rather minor morphological distinctions which may be used to distinguish these species are shown diagrammatically in Figure 14 in relation to their geographic distribution. These five well-defined taxa may represent no more than geographic races within a morphologically variable species, but until additional data are available it is best to retain these forms as distinct species.

External morphology. Except for the specialized semiarboreal forms on Hispaniola, the members of the *cantherigerus* species assemblage are very similar to each other in most external characters. Several forms such as *ater* (Jamaica) and the *ferox* populations from the southwest peninsula of Haiti (for which the name *scalaris* Cope is available) have lost the loreal scale, but this has occurred repeatedly in many groups and cannot be considered more than a specific or subspecific difference. All the members of this group are similar in size, most falling between 800 and 1300 mm in total body length. There are always eight supralabials, usually with the third, fourth, and fifth entering the orbit. The number of dorsal scale rows ranges from 17 to 23. Ventral scale counts range approximately between 160 and 230, and caudal counts roughly between 100 and 150. The anal plate is usually divided, but may be
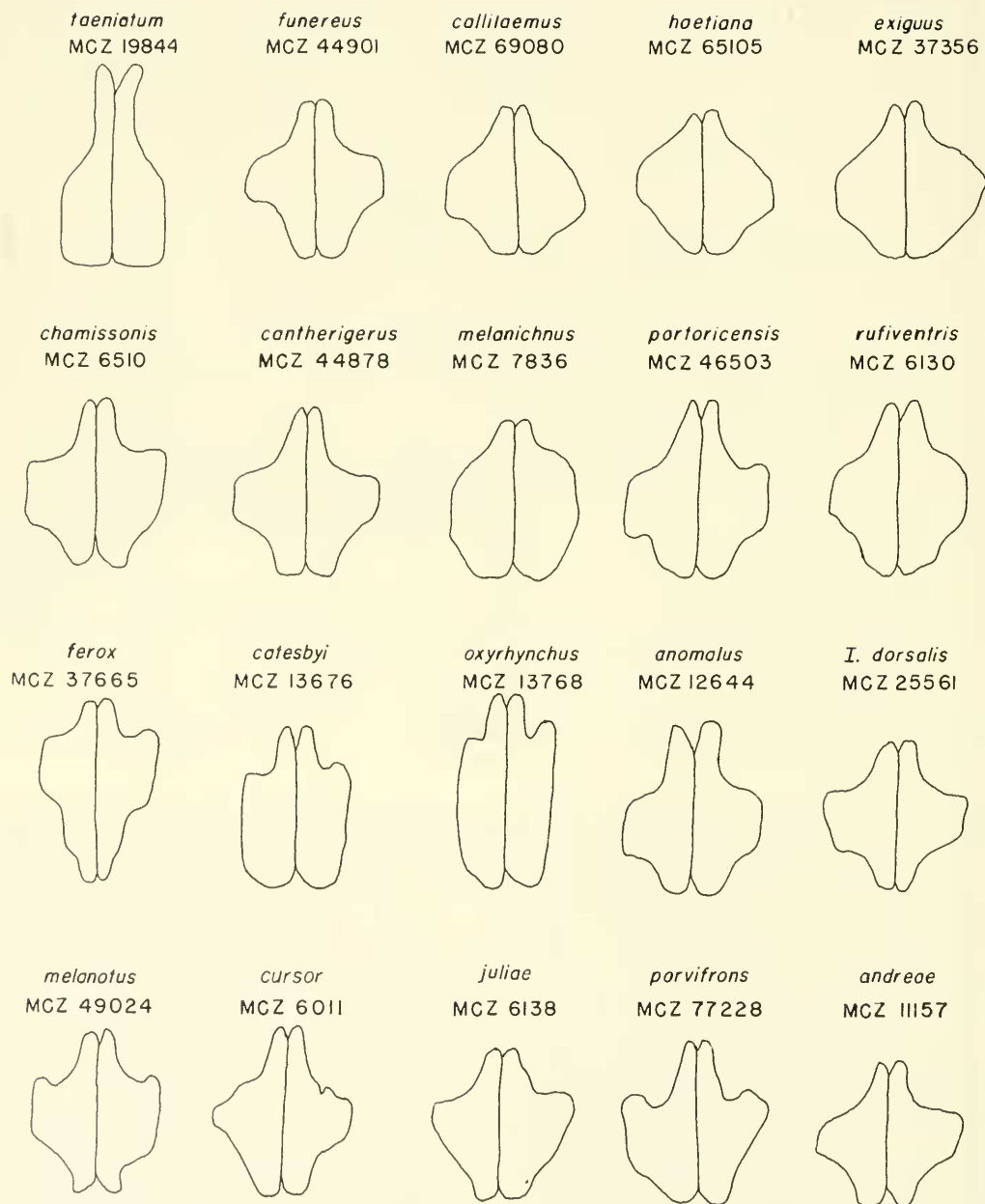
Fig. 12. Shape of the nasal banes for representative species of the four species assemblages of West Indian colubrid snakes as discussed in the text. Not to scale. Approx. × 7.
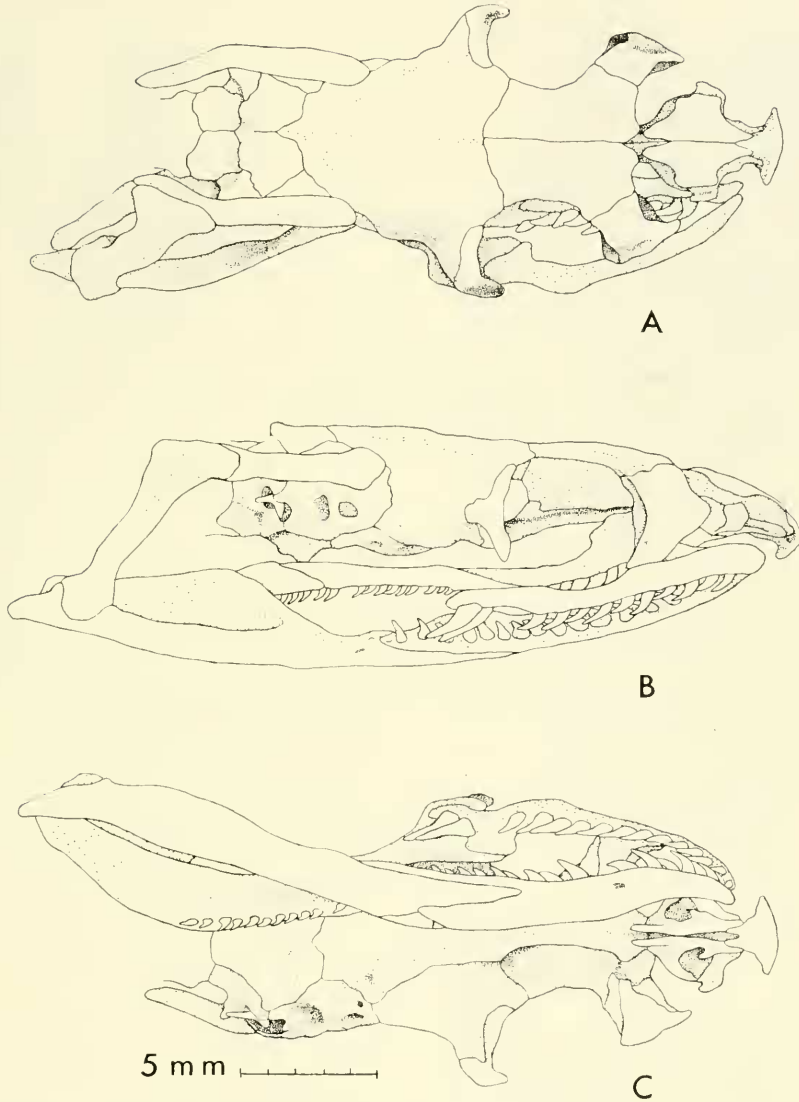
Fig. 13. Skull structure of *Alsophis portoricensis*, MCZ 46503. A, dorsal view; B, lateral view; C, ventral view.

single in some specimens of *sancticrucis* (Schwartz, 1966). The Hispaniolan species *ferox* has a single apical pit on the dorsal body scales, whereas *catesbyi, oxyrhynchus, dorsalis,* and *frenatus* have none. The remaining species have two pits.

The species *ferox* differs externally from other members of the assemblage. The snout is elongated, the rostral scale forms

an acute angle with the top of the head, and the eye is large and bulging. The pupil shape in *ferox* is usually oval, but out of 28 preserved specimens from the southwest population, 26 had round or irregularly rounded pupils, and only one individual had a distinctly oval pupil in both eyes.
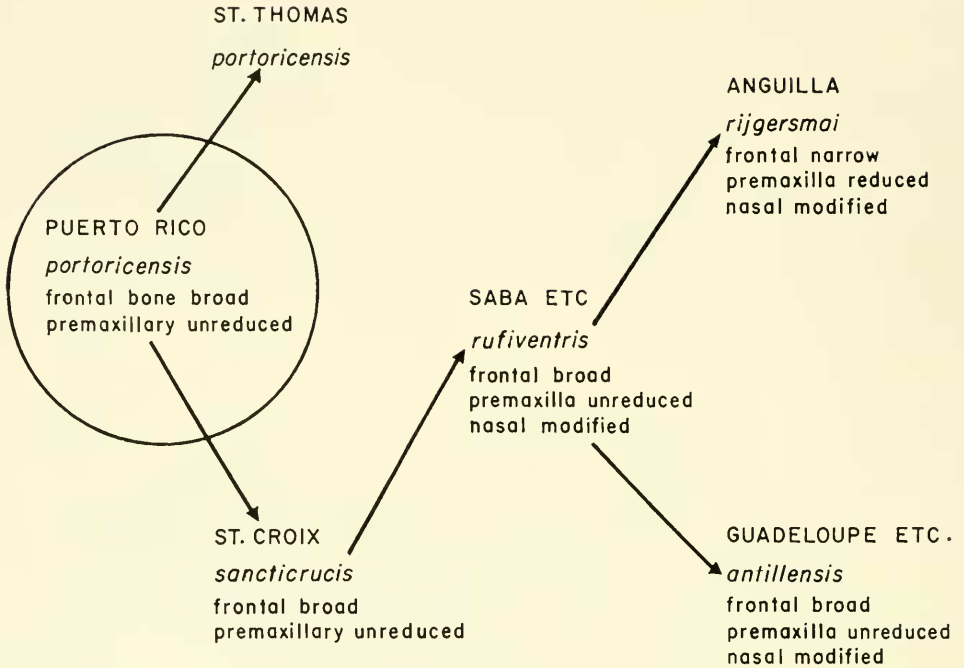
The arboreal species of Hispaniola,

ST. THOMAS

portoricensis

ANGUILLA

rijgersmai
frontal narrow
premaxilla reduced
nasal modified

PUERTO RICO

portoricensis
frontal bone broad
premaxillary unreduced

SABA ETC

rufiventris
frontal broad
premaxilla unreduced
nasal modified

ST. CROIX

sancticrucis
frontal broad
premaxillary unreduced

GUADELOUPE ETC.

antillensis
frontal broad
premaxilla unreduced
nasal modified

Fig. 14.   Geographic distribution of several morphological characters within the *portoricensis* subgroup of the *cantherigerus* species assemblage.   Circle represents the supposed center of dispersion of this group.

catesbyi, oxyrhynchus, dorsalis, and *frenatus,* are clearly united in a well-defined subgroup. All, except *catesbyi,* are long, slender, and clearly adapted for tree living. A recent study by Horn (1969) demonstrates the specific synonymy of *"wetmorei"* with *frenatus* and of *"scandax"* with *catesbyi.*

The subspecies *vudii utowanae* as described by Barbour and Shreve (1938) has a higher ventral and subcaudal scale count than other races of *vudii.*

Hemipenis. The structure of the hemipenis is remarkably uniform within the *cantherigerus* assemblage. The sulcus spermaticus is divided near the base of the organ and each branch extends to the tip of one lobe of the deeply bifurcated apex (Fig. 15). Several rows of longitudinally arranged stout spines are present along the middle one half of its length; these grade into numerous smaller spines basally. The

base may also be nude or have long plicae. The sulcus is bordered by a fringe of folded tissue bearing modest sized, closely spaced spines that grade into smaller ones distally. On the apex of each lobe, a reticulate network of tissue surrounds the sulcus, with moderate to long filiform papillae (papillate calyces). These calyces usually grade into the surrounding tissue proximally, but may form a more or less well-defined capitate structure as in *protoricensis, rijgersmai,* and *antillensis.* The hemipenis in *ferox* does not differ from that of other species in this group except in having longer apical papillae. In *catesbyi* and the other arboreal snakes of Hispaniola the hemipenis is proportionately shorter than, but basically similar to, that of *cantherigerus.* It is more heavily spinose, and the apical papillae on the sulcate surface extend further basally to the point of division of the sulcus.
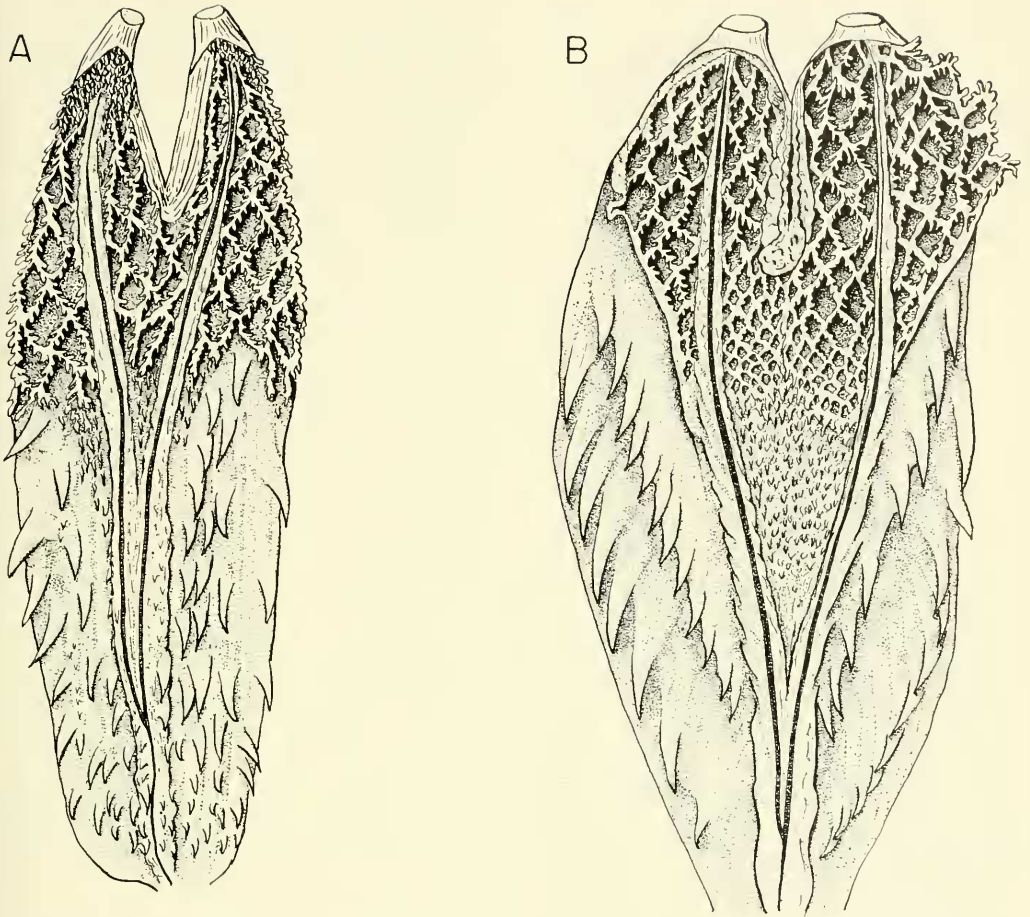
Fig. 15. Hemipenis morphalogy in the *cantherigerus* species assemblage; semidiagrammatic. Organ is uneverted and dissected *in situ*. A, *Alsaphis ater*, MCZ 6005; B, *Alsaphis portaricensis*, MCZ 58804. Approx. × 5.

Mainland relationships and origin of the group. Examination of South and Central American genera has revealed several that are morphologically very close to the *cantherigerus* species assemblage. Of the four mainland species customarily referred to the genus *"Dromicus,"* three are clearly related to the present group; these are *chamissonis*, *tachymenoides*, and *angustilineatus*. The fourth species, *"Dromicus" amazonicus*, is allied to the *melanotus* species group to be discussed below.

The species *tachymenoides* (Peru) and *angustilineatus* (Peru) differ from *chamis-* *sonis* (Chile and Argentina) only in several minor characters, and what is said below about the latter will apply also to these two species. The major distinction between *chamissonis* and *cantherigerus* (Cuba) is the lower number of teeth in the former (see appendix); in all other skull characters the two are extremely close. Externally there are no differences which would argue against a close relationship, although the mainland species have only one pit on each dorsal body scale. In the structure of the hemipenis the sulcus spermaticus is less deeply divided in *chamissonis*, but the
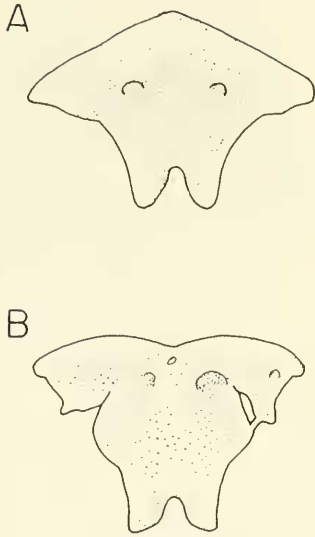
Fig. 16. Premaxilla in a typical West Indian species of the *cantherigerus* species assemblage compared with that bone characteristic of the Galapagos species of this group. A, *Alsophis cantherigerus*, MCZ 8611; B, *Alsophis slevini*, MCZ 28470. Ventral view. Approx. × 12.

arrangement of spines and the nature of the apical differentiation is similar to that of the Cuban form. As a whole, *chamissonis* must be considered as a mainland representative of the *cantherigerus* assemblage.

Two other mainland genera showing a close relationship to the *cantherigerus* group are *Philodryas* from South America and *Conophis* from Central America. Osteologically these genera are very close to *chamissonis*, except that both have well-developed grooves on the posterior maxillary teeth. Externally *Philodryas* may have one or two apical pits per dorsal body scale, and *Conophis* has none, but in size, scale pattern, and scale count they do not differ significantly from *chamissonis*. The structure of the hemipenis in both genera is of the *cantherigerus* type, with a deeply forked sulcus, lateral spines, and an apical ornament of papillate calyces arranged as in that group.

The present distribution of *chamissonis*,

tachymenoides, and *angustilineatus* makes it difficult to derive any part of the West Indian fauna from them unless we postulate a former widespread distribution for an ancestral group. *Philodryas* and *Conophis* now occupy the geographic areas which the ancestral genus must have inhabited if the West Indian representatives of this group were derived by waif dispersal from the mainland. However, the presence of rear fangs in these two genera would appear to preclude them from any direct ancestry to the nonfanged Antillean group. The morphological relationships between *Philodryas, Conophis*, and *chamissonis*, etc., as well as their present distributions, suggest a widespread ancestral group common to all three. The species *chamissonis, tachymenoides*, and *angustilineatus* may represent relatively undifferentiated relicts of that ancestral group, and *Philodryas* and *Conophis* specialized rear-fanged descendants. The development of rear fangs has occurred repeatedly in a number of unrelated groups and is no bar to the relationship here suggested. If such a specialization was of selective advantage over the nonfanged condition, we might expect these forms to have displaced the ancestral type from much of its former range.

Taxonomy. The *cantherigerus* species assemblage as defined above on the basis of osteological and hemipenial characters may be expanded to include *chamissonis, tachymenoides*, and *angustilineatus* from South America. The three species from the Galapagos referred to the genus "*Dromicus*" must also be placed here. These three species—*biserialis, dorsalis*, and *slevini*—are very much like the present assemblage in external characters, osteology, and hemipenial morphology. However, they are clearly closer to each other, and represent products of speciation on the Galapagos. The dental formula is similar in all three forms and is as low as in their mainland relatives (appendix). A minor but distinctive character which sets these forms apart
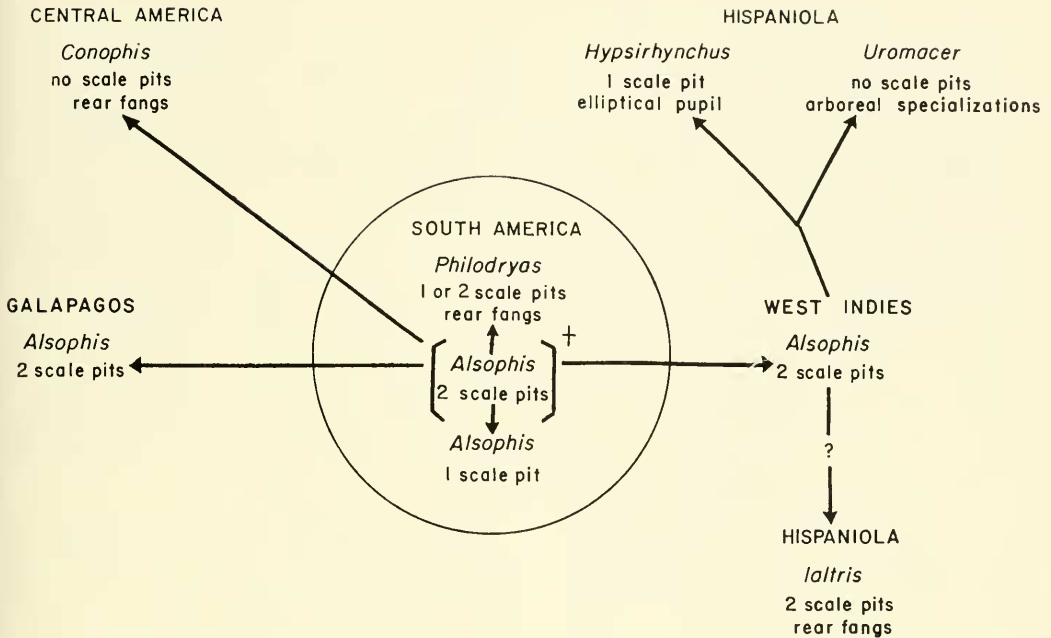
CENTRAL AMERICA

Conophis
no scale pits
rear fangs

HISPANIOLA

Hypsirhynchus
I scale pit
elliptical pupil

Uromacer
no scale pits
arboreal specializations

SOUTH AMERICA

Philodryas
I or 2 scale pits
rear fangs

GALAPAGOS

Alsophis
2 scale pits

Alsophis
2 scale pits

+

WEST INDIES

Alsophis
2 scale pits

Alsophis
I scale pit

?

HISPANIOLA

Ialtris
2 scale pits
rear fangs

Fig. 17. Geographic distribution of several morphological characters in the genus *Alsophis* and in two related mainland genera. The circle represents the supposed center of dispersion for this group. The † symbol indicates that the ancestral form of *Alsophis* is extinct on the mainland.

from other members of the *cantherigerus* group is the shape of the premaxilla (Fig. 16); here this element is depressed anteriorly in the midline so that the lateral processes appear to curve forward and then back in a winglike fashion.

Within the West Indies as discussed above, *utowanae* from Great Inagua is somewhat distinct from other subspecies of *vudii*. At the time of writing only two specimens including the type were available for study. Although the differences of these two specimens from *vudii vudii* appear to be more than subspecific, it seems advisable to retain *utowanae* as a subspecies of *vudii* until additional specimens are available and the range of variation better known.

The four arboreal species on Hispaniola –*catesbyi, oxyrhynchus, dorsalis,* and *frenatus*–are unquestionably closely related and united morphologically; they form the well-defined genus *Uromacer*. The Hispan-

iolan species *ferox* is osteologically undifferentiated from other members of the group except for its enlarged teeth, and in many ways it is intermediate between *ater* (Jamaica) and *Uromacer catesbyi*. Mertens (1939) favored retention of *ferox* in a distinct genus *(Hypsirhynchus)* because of its elliptical pupil in contrast to the rounded pupil of "*Dromicus.*" However, variation between *ferox* from the southwest population and *ferox* from other areas on Hispaniola with respect to pupil shape makes this character suspect for use on the generic level in this group until more is known concerning postmortem effects on this structure. Nevertheless, the other peculiarities of *ferox*, such as its enlarged teeth and unusual head shape, probably warrant retention of the currently recognized genus *Hypsirhynchus*. The consistent absence of a loreal scale in the populations from the southwest peninsula of Haiti, plus the suggestion of a distinction in pupil

shape, justify the use of the subspecific name *ferox scalaris* for them.

Dunn (1932) divided the remaining species of the present *cantherigerus* assemblage into two additional genera based on the number of apical pits on the dorsal body scales: *Alsophis* was distinguished as having two pits and *Dromicus* one pit.

An examination of the relationships within the *cantherigerus* assemblage in the present study indicates that scale pit number may or may not be consistent with other characters at the generic level, and therefore cannot always be used to define major taxa. The genus *Hypsirhynchus* has one pit and the six species of *Uromacer* have none. The remaining West Indian species have two pits side by side at the tip of the dorsal body scales, whereas on the mainland, *chamissonis, angustilineatus*, and *tachymenoides* have a single apical pit. The three Galapagos species have two pits. The distinction between *Philodryas* and *Conophis* made by Boulenger (1896) was based on the presence of one apical pit in the former and none in the latter. Osteologically these two genera are very close but, since a detailed analysis of these groups was not made as part of the present study, they are here considered provisionally distinct genera. The geographic distribution of scale pits and their suggested phyletic relationships are shown in Figure 17, along with several other characters. From the evidence one might reasonably infer a primitive condition of two scale pits with reduction as indicated in the figure.

Scale pits have served, in the past, to diagnose groups based on this feature alone. However, it is clear from other characters that the use of scale pits to define major groups may result in oversplitting of otherwise closely related assemblages. With the recognition that scale pits by themselves are useful as taxonomic characters within this group only at the species or species-group level, the West Indian species of the *cantherigerus* assemblage (excluding *Hypsirhynchus* and *Uromacer*) may be considered congeneric with *chamissonis, angustilineatus*, and *tachymenoides* from South America, and with *dorsalis, biserialis*, and *slevini* on the Galapagos archipelago.

Smith and Grant (1958) have shown that Bibron's (1843) type of *Dromicus* was *cursor* from Martinique. This is a form unrelated to South American "*Dromicus*," as I will show below. With the name *Dromicus* thus unavailable, the present assemblage of species is referred to *Alsophis* with the type *antillensis* (= *leucomelas*) Fitzinger. (See Brongersma, already cited above, for the identity of the name *antillensis*.)

The suggested phyletic relationships between the genera and species of the *cantherigerus* assemblage are shown in Figure 18.

Zoogeography. Two lines of evidence indicate a western origin for the *cantherigerus* species assemblage into the West Indies. First, *Alsophis cantherigerus* from Cuba is the Antillean species most similar to *A. chamissonis* of the mainland; this similarity is most notable in osteological characters and especially in the dental formula, which in these two species is the lowest of the whole assemblage. The Galapagos forms, likewise, have relatively few teeth, as do the suggested mainland derivatives *Philodryas* and *Conophis*. Within the West Indies a general trend toward increased number of teeth is evident, especially in the specialized arboreal species of *Uromacer*, and in the *portoricensis* species group. From the geographic distribution of dental formulae, it would appear that a low number of teeth is primitive for the mainland ancestor of this assemblage. In other characters also, the more easterly distributed species show a greater divergence from the mainland forms, thus tending to support the view that the group entered from the west.

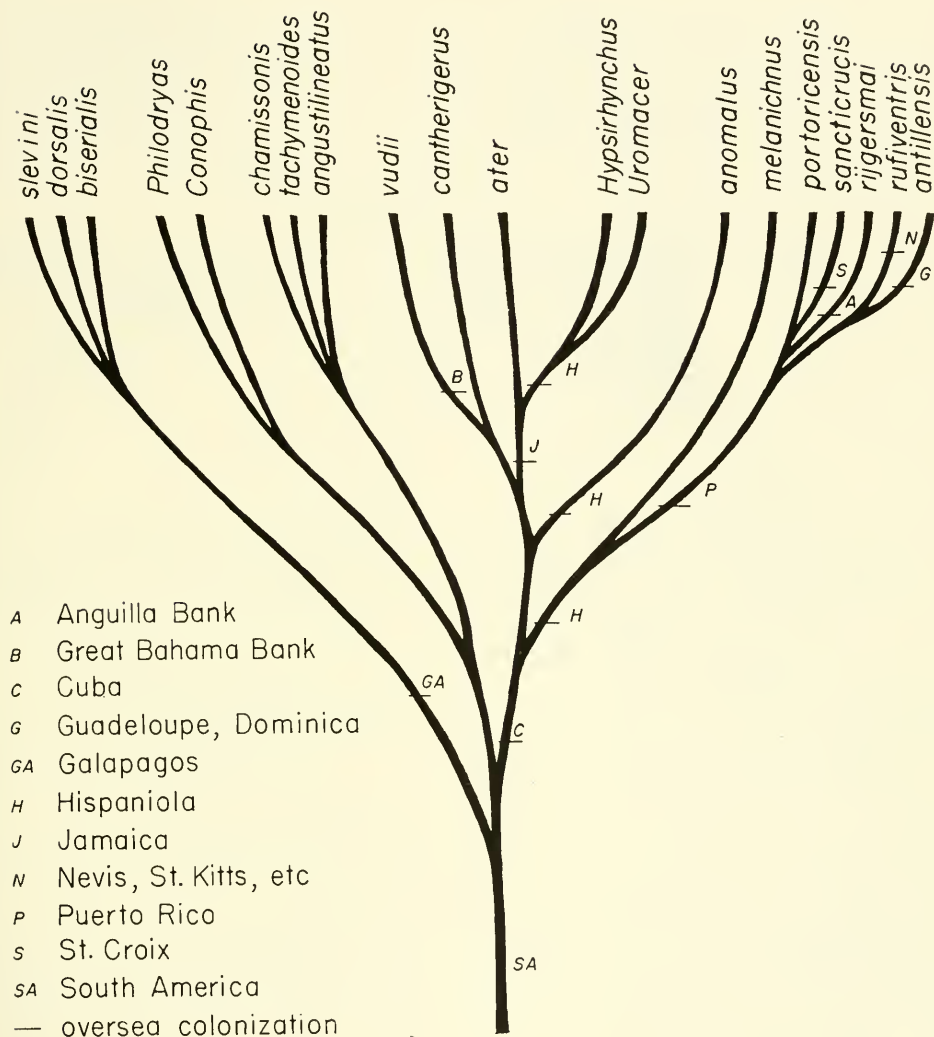The second line of evidence indicating a western origin is that no member of this

Fig. 18. Suggested phyletic relationships between species of the *cantherigerus* species assemblage and related genera. Short horizontal lines indicate proposed oversea colonizations. Geographic distributions as indicated by lettered symbols.

species assemblage occurs on the Lesser Antilles south of Dominica. This in itself is not significant since, as Gorman and Atkins (1969) have shown for *Anolis*, colonization does not necessarily proceed sequentially island by island along the chain of the Lesser Antilles. Nevertheless, taken with the first line of evidence, this assumes more importance.

The following zoogeographical history for the genus *Alsophis* may be suggested. The assemblage appears to have been derived from an ancestral species probably not unlike *Alsophis cantherigerus* in its osteological, hemipenial, and external morphology. From this widely distributed ancestral group in South America (and probably Central America as well), a single trans-Caribbean colonization could have resulted in the establishment of this group
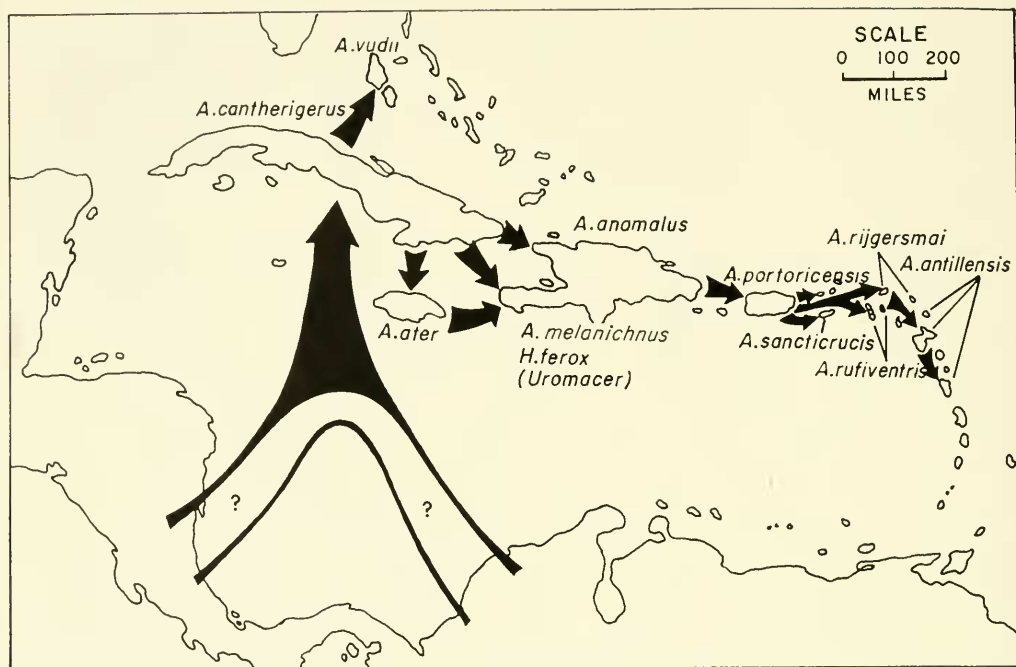
Fig. 19. Proposed routes of colonization of the West Indies by the *cantherigerus* species assemblage. The arrows are not intended to represent exact paths. The distribution of extant species and genera is as indicated. It is not certain whether this group entered from Central or South America.

on Cuba. This was followed by a subsequent dispersion and radiation to Jamaica *(ater)*, the Little and Great Bahama banks *(vudii)*, and Hispaniola *(melanichnus)* (Fig. 19). From Hispaniola an early stage of *melanichnus* gave rise to *portoricensis* on Puerto Rico. The four species of the Virgin Islands and Lesser Antilles, *sancticrucis, rufiventris, rijgersmai,* and *antillensis,* appear to be part of a relatively recent radiation of *portoricensis,* with differentiation on these geographically isolated islands. The remaining history of the group involves a series of inter-island colonizations to centrally placed Hispaniola from the more peripheral islands of the Greater Antilles. A second migration from Cuba by an early stage of *cantherigerus* seems best to account for *anomalus,* which shows a closer affinity to the Cuban species than to *melanichnus* (Hispaniola). Alternatively, a back colonziation from Puerto Rico may

have resulted in *anomalus.* The rather peculiar *Hypsirhynchus ferox* is close to *ater* (Jamaica) with respect to its skull and hemipenis and possibly represents a Jamaica-Hispaniola migration, with subsequent specialization of *Hypsirhynchus* resulting in its external differences. Another endemic genus on Hispaniola, *Uromacer,* may have been derived from an early form of *H. ferox* before the latter achieved its peculiar specializations.

Because of its central location, Hispaniola has received a greater number of species than any of the other islands, and it may have been competition between these species that led to the specializations of some of them. The giant form *anomalus,* the arboreal species of the genus *Uromacer,* and *Hypsirhynchus* may have differentiated as a means of dividing up the habitat more efficiently. Competition among closely related and overlapping species

MAXILLARY TEETH

PTERYGOID TEETH

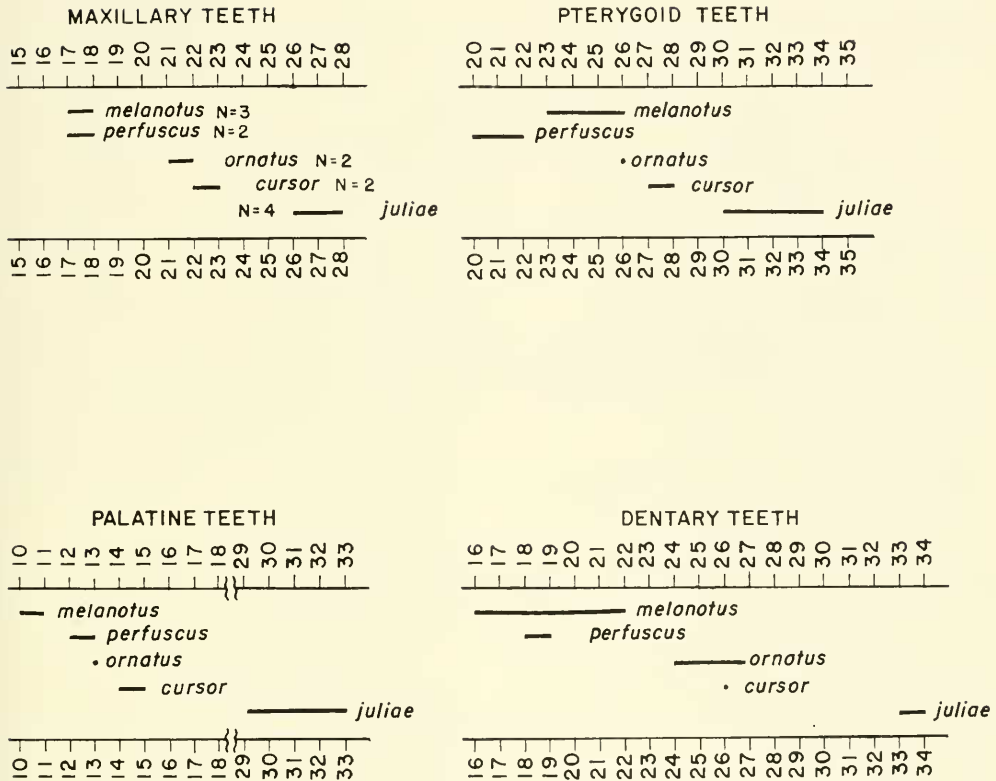**PALATINE TEETH**

DENTARY TEETH

Fig. 20. Observed ranges of variation in numbers of teeth on each tooth-bearing element for the five West Indian species of the *melanotus* species assemblage.

often results in the well-known phenomenon of character divergence whereby the competing forms become adapted (first ecologically, then morphologically) to somewhat different aspects of the environment, thus reducing competition. It is interesting to note that, even in the relatively less specialized Hispaniolan species *anomalus* and *melanichnus,* character divergence has progressed to a remarkable degree, so that these forms lie near the two extremes of variation for the entire assemblage in many of their characters (see Figs. 6, 8, 9, and 11).

Another waif dispersal from the mainland to the Galapagos almost certainly resulted in the differentiation of *biserialis, dorsalis,* and *slevini* on these islands. Later,

rear-fanged specialization within the ancestral mainland genus possibly led to *Philodryas* and *Conophis* which displaced their antecedent from much of its former range. The three closely related species, *chamissonis, tachymenoides,* and *angustilineatus,* have remained as relatively unmodified relicts of the original mainland stock, except for reduction in the number of scale pits.

MELANOTUS SPECIES ASSEMBLAGE

Included West Indian species: *cursor* LACÉPÈDE, Martinique; *juliae* (including *mariae*) COPE, Guadeloupe, Marie Galante, Dominica; *melanotus* SHAW, South America, Trinidad, ? Grenada; *ornatus* GARMAN, St. Lucia; *perfuscus* COPE, Barbados.
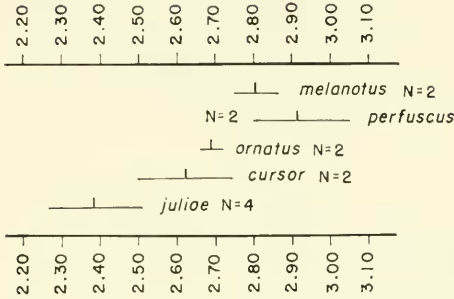
Fig. 21. Skull length/width indices for the five West Indian species of the *melanotus* species assemblage. Widths are taken at the otic region of the skull.

Osteology. This assemblage of species is distributed from the island of Guadeloupe south to Trinidad. It is distinguished from the *Alsophis cantherigerus* species assemblage and other Antillean xenodontines primarily by the shape of the prefrontal bone and by the structure of the hemipenis (discussed below). The prefrontal is long dorsoventrally and narrow anteroposteriorly with a sharply pointed anterior projection at about midlength (see Fig. 5).

The species for which this group is named, *melanotus*, occurs on Trinidad and Tobago and has been questionably reported from Grenada. It also occurs in Venezuela and Colombia. Like all members of this group *melanotus* is about half the size of *A. cantherigerus* and contrasts with it in the following skull characters: the postorbital region is proportionately longer; the frontal bone is relatively shorter anteroposteriorly with very little emargination above the orbits; the skull is considerably more flattened dorsoventrally as compared with its width; as a result of the latter character, the interorbital partition formed by the parasphenoid bone is shorter in its dorsoventral extension; long, thin lateral processes extend back from the premaxilla in contrast to the short, wide based processes of *A. cantherigerus*. The dental formula for *melanotus* is about 15 + 2 maxillary, 10 palatine, 24 pterygoid, and 19 dentary teeth (Fig. 20 for variation).

The skull of the endemic species *perfuscus* on the island of Barbados is proportionately longer and narrower than that of *melanotus* (Fig. 21). The supratemporal and quadrate bones are more elongated and comparatively narrower. The orbit is small. The postorbital bone lies far forward on the parietal and is nearly in contact with the frontal. In this last character *perfuscus* is distinct from other members of the present group; in the latter, a wide expansion of the parietal bone separates the postorbital from the frontal. In general skull proportions and in its low dental formula, *perfuscus* is closer to *melanotus* and other mainland representatives of this assemblage than it is to other Antillean species on adjacent islands.

The species *ornatus* from St. Lucia is slightly larger than *melanotus* (Trinidad) and has a somewhat broader skull. The prefrontal bone is of the *melanotus* type, but is wider than in that species. In most other skull characters the two forms are very similar except for the dental formula, which is higher in *ornatus*. Clearly related to the latter is the species *cursor* from Martinique (Fig. 22), which differs only in the smaller size of the nasal bone. On Guadeloupe, Dominica, and Marie Galante the species *juliae* has a higher dental formula than *cursor*, and the supratemporal, quadrate, and premaxilla are greatly reduced in relative size. A similar reduction is seen in some related mainland species such as *bimaculatus*, but this probably represents parallelism rather than an independent derivation from one of these mainland forms.

It is surprising that no member of this group has been reported from St. Vincent. This island forms an important intermediate stepping stone between Grenada and St. Lucia. The mongoose is widespread on this island, and it is possible that a formerly present species, endemic or not, has become extinct.

External morphology. Externally the *melanotus* species assemblage is a homo-
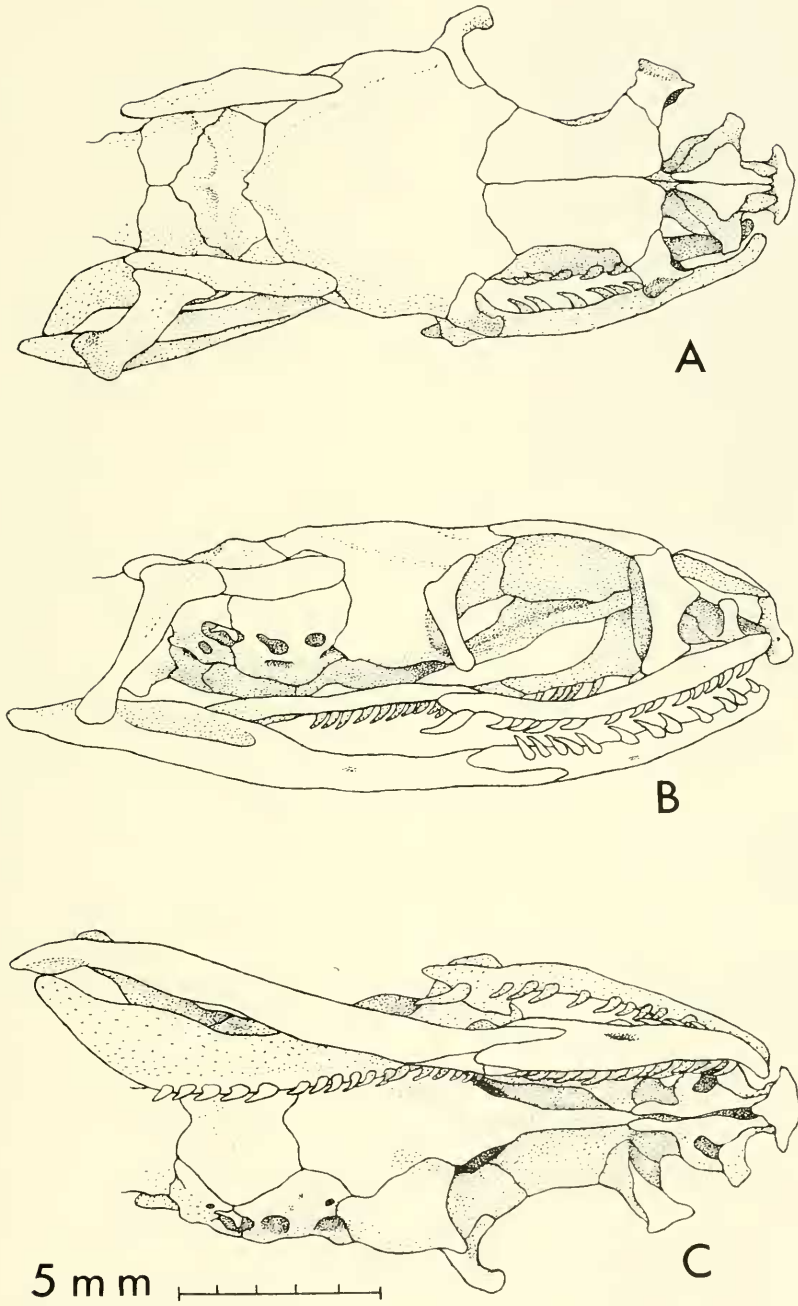
Fig. 22. Skull structure of *Dramicus cursor*, MCZ 6011a reversed). A, dorsal view; B, lateral view; C, ventral view.
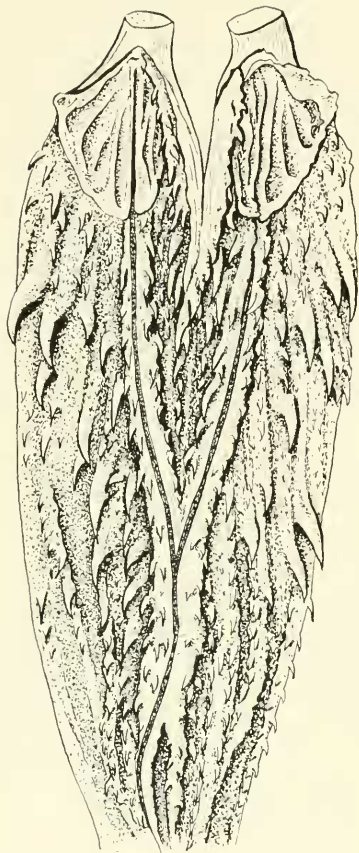
Fig. 23. Hemipenis morphology in *Dromicus cursor* (MCZ 6011) showing the typical apical own of the *melanotus* species assemblage; semidiagrommatic. The organ is uneverted and dissected *in situ*. Approx. × 5.

geneous one and in many respects is similar to the *cantherigerus* assemblage. As in the latter group there are eight supralabials, but here only the fourth and fifth enter the orbit. The number of scale rows may be 17 or 19, and the ventral scales number approximately between 150 and 200. In contrast to *Alsophis*, the number of subcaudals is rarely over 100. The anal plate is divided. All of these snakes are moderate in size and are roughly between 600 and 1000 millimeters in total body length. A single apical pit is usually present on the dorsal body scales, but may be absent as in *juliae mariae*.

Hemipenis. The hemipenis of *cursor* (Fig. 23) is shorter proportionately than in *Alsophis cantherigerus*, and the sulcus spermaticus is less deeply divided. As in that species, several rows of stout spines extend along the sides of the organ but, in contrast to it, small spines are also present between the diverging branches of the sulcus. The organ is generally weakly bifurcated and the apical ornament is distinct from all other West Indian xenodontines. Here papillae are never present; instead, a series of membranous folds radiate from the apex and terminate in a transverse fold of tissue which encircles the tip of each lobe. This fold forms a well-defined apical disk on each lobe when the organ is everted. The sulcus forks and proceeds onto the disk and to the tip of each lobe.

The structure of the hemipenis in the other species in this assemblage is essentially like that of *cursor*.

Origin and Zoogeography. The *melanotus* group offers no problem of origin. This well-defined and closely related assemblage is morphologically continuous with the widespread series of species currently referred to the genus *Leimadophis*, common on the mainland.[1] In both its osteology and hemipenial morphology the type species of *Leimadophis*—*L. almadensis*—is clearly allied to the present group, and there are no external characters which would preclude such a relationship. It seems probable that a northward colonization of the Lesser

[1] *Dromicus amazonicus* is known only from the type specimen, MCZ 2820, and may also be referred to the present group. Its prefrontal bone is essentially of the *melanotus* type and the hemipenis has a weak apical disk. In all its osteological characters this specimen may be distinguished from other members of the present group only in having those features, such as broad skull, thin cranial bones, low, rounded crests, etc., which normally characterize juvenile specimens. Even the relatively weak disk on the hemipenis probably reflects the youthful condition of the specimen. It is thus quite possible that this form represents an immature specimen of a previously described South American species of the present assemblage.
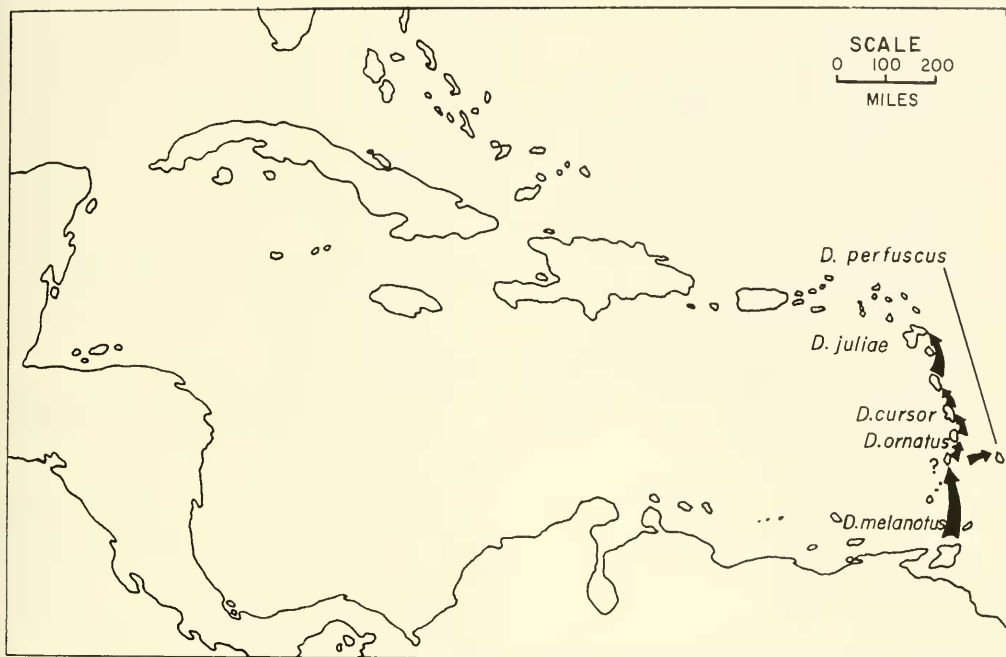
Fig. 24. Proposed routes of colonization of the West Indies by the *melanotus* species assemblage. Distribution of extant species is as indicated.

Antilles by a mainland species similar to *melanotus* occurred in relatively recent times. From this species or its ancestor, *ornatus* (St. Lucia) was almost certainly derived, possibly via a now extinct intermediate species on St. Vincent. Successive overseas migration (Fig. 24) probably resulted in *cursor* on Martinique and *juliae* on Guadeloupe, Dominica, and Marie Galante. The Barbados species, *perfusens*, appears to have been derived from one of the islands to the west, perhaps from St. Vincent or Grenada.

Taxonomy. As mentioned above, Smith and Grant (1958) have shown that Bibron's (1843) type of *Dromicus* was *cursor*. With *cursor* and *almadensis* here considered as congeneric, *Dromicus* Bibron 1843 and *Leimadophis* Fitzinger 1843 become synonymic names for this assemblage. Although the actual dates of publication of these two names remain in question, December 31, 1843, is now to be taken as the official publication date of Fitzinger's *Systema*

Reptilium (Smith and Grant, 1958), and Bibron's *Dromicus* thus becomes the senior synonym for the present assemblage with *Dromicus cursor* as the type species.[1]

The genus *Dromicus* is very similar to the South American genus *Liophis* Wagler 1830. In all of the characters studied, Wagler's type of *Liophis*—*L. cobella*—is close to the present assemblage. The prefrontal is like that of *D. melanotus*, the frontal is short with very little emargination above the orbits, and the interorbital partition is very small. The hemipenis of *Liophis* has a pair of well-developed apical disks as in *D. melanotus*, but differs in the presence of basal hooks (Roze, 1964). Body

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[1] After the present paper was in manuscript form, it was brought to my attention that Drs. Albert Schwartz and Richard Thomas reached the conclusion of "*Dromicus*" cf. *cursor* – *Leimadophis* synonymy independently of the present author. Their conclusion was reported in a letter to Dr. E. E. Williams.
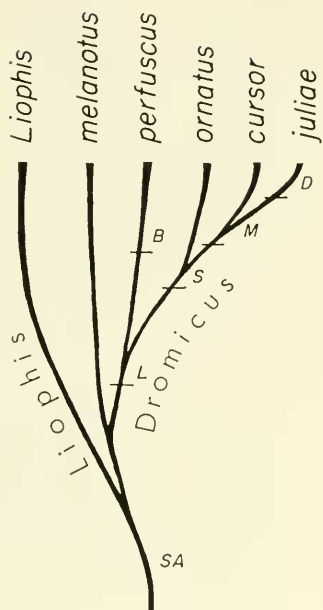
B   Barbados
D   Dominica
L   Lesser Antilles
M   Martinique
S   St Lucia
SA   South America
—   oversea colonization

Fig. 25. Suggested phyletic relationships between species of the *melanotus* species assemblage and the genus *Liophis*. Short horizontal lines indicate proposed oversea colonizations.

size and scale counts are within the range of *Dromicus* (present concept).

The question arises as to the validity of the generic distinctions between "*Leima-dophis*" (i.e., *Dromicus*) and *Liophis* made by Roze (1964: 535). As we have seen, the presence or absence of scale pits may not be as important a distinction as formerly believed. Thus, the only major difference between these two genera is in the maxillary dentition in which "*Leim-adophis*" has a diastema with much en-

larged posterior teeth, whereas *Liophis* lacks a diastema and the posterior teeth are little enlarged (Roze, 1964). I suspect that these two groups will be considered as congeneric when better known, but on present evidence I here treat them as valid genera.

The inferred phyletic relationships between *Liophis* and the West Indian species of *Dromicus* are presented in Figure 25.

ANDREAE SPECIES ASSEMBLAGE

Included West Indian species: *andreae* REINHARDT AND LÜTKEN, Cuba; *parvifrons* COPE, Hispaniola.

Osteology. Only two species of this assemblage are extant in the West Indies, *andreae* on Cuba and *parvifrons* on Hispaniola and nearby islands. They are generally considerably smaller in size than *Alsophis* and are about the size of *Dromicus melanotus*. In cranial osteology *andreae* and *parvifrons* show features characteristic of both *Alsophis* and *Dromicus* (Fig. 26). The frontal bones are very long and narrow with a deep emargination above the orbits as in *Alsophis*, but unlike the proportionately shorter and wider frontals of *Dromicus* (see Fig. 3). On the contrary, in the structure of the prefrontal bone, the present assemblage is close to *Dromicus* with a long and narrow prefrontal bearing a sharply rounded anterior process. This is quite distinct from the relatively wider prefrontal of *Alsophis* in which the anterior surface is broadly rounded and the bone is proportionately wider (see Fig. 5). In general skull proportions *andreae* and *parvifrons* are closer to *Alsophis* than to *Dromicus*. The parasphenoid bone is very narrow as in *A. cantherigerus* and other westerly distributed species of *Alsophis*, as well as mainland forms, but unlike the rather broad shape of that bone in the *A. portoricensis* species group or in *Dromicus*. The parasphenoid partition between the orbits extends high above the trabecular canals, as in most species of *Alsophis* except
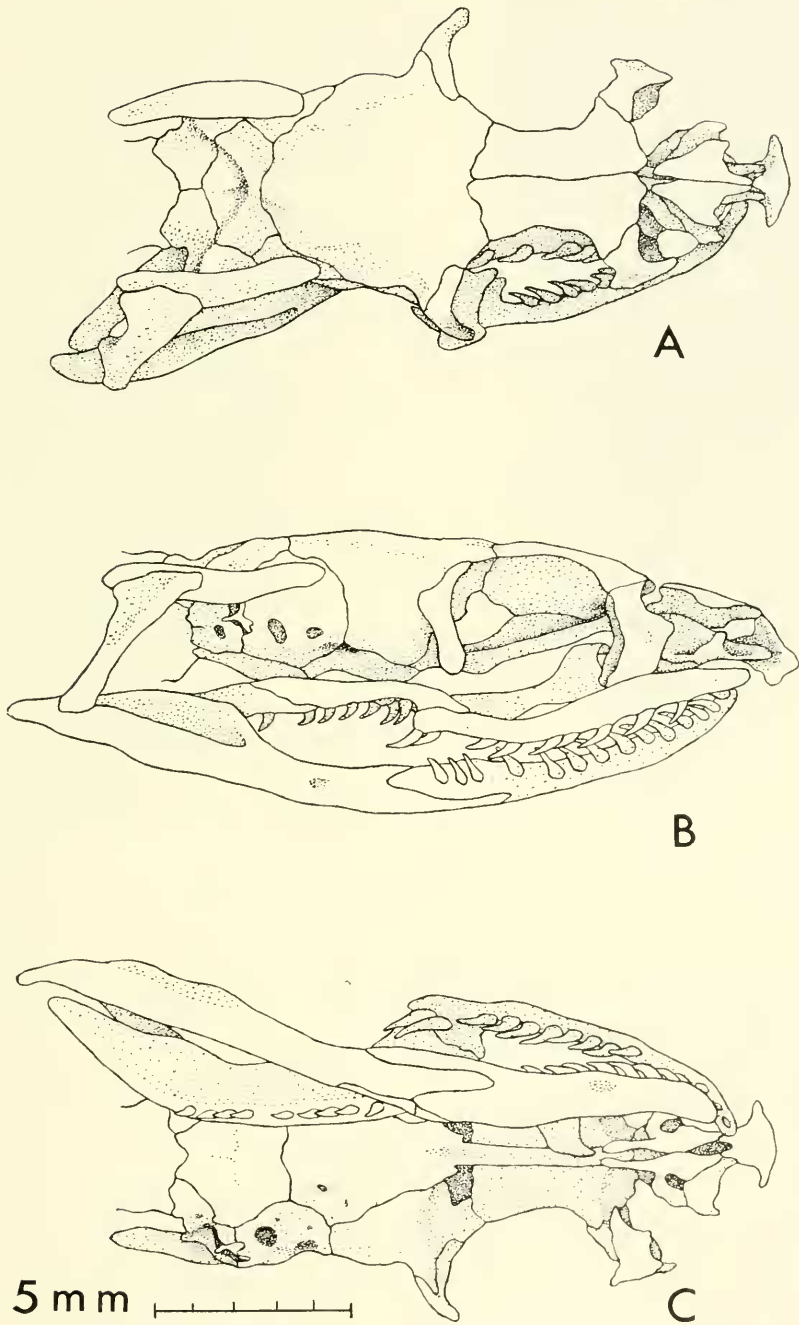
Fig. 26. Skull structure of *Antillophis parvifrons* nov. gen., MCZ 77228. A, dorsal view; B, lateral view; C, ventral view.
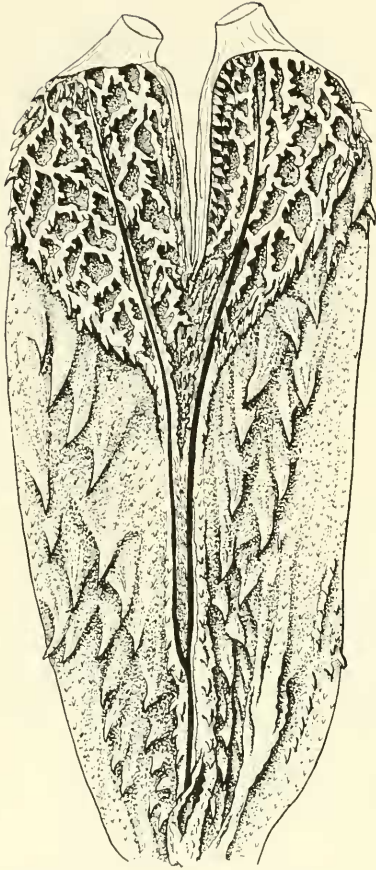
Fig. 27. Hemipenis morphology in *Antillophis parvifrons* nov. gen., MCZ 60064; semidiagrammatic. The organ is uneverted and dissected *in situ*. Approx. × 5.

portoricensis and related species. The premaxillary bones in *andreae* and *parvifrons* lack the long lateral process as in *Dromicus*.

The dental formulae in these two species is comparable to that of both *Alsophis* and *Dromicus*; that is, about 16 + 2 maxillary, 12 palatine, 26 pterygoid, and 21 dentary teeth in *parvifrons*, and 21 + 2 maxillary, 16 palatine, 35 pterygoid, and 26 dentary teeth in *andreae*.

Nonosteological characters. In external characters *andreae* and *parvifrons* are similar to *Dromicus*. The number of ventral scales is generally lower for these species than in *Alsophis* and about the same as in *Dromicus*. The subcaudal scale number in *parvifrons* is higher than that of *andreae* and of species of *Dromicus*, while it is within the normal range for species of *Alsophis*.

In the present assemblage, each dorsal body scale bears a single sensory pit in contrast to the two pits in all West Indian species of *Alsophis*, and in this respect is like most species of *Dromicus*.

It is in the structure of the hemipenis, however, that *andreae* and *parvifrons* depart radically from *Dromicus*. Here the organ has a deeply divided sulcus spermaticus, bordered by a thick fold of spinose tissue. Several rows of stout spines parallel the sulcus, each branch of which terminates on a diskless apex bearing long filiform calyces (Fig. 27). There are no basal hooks, neither are there spines between the branches of the sulcus spermaticus as in *Dromicus*. This structure is basically like that of *Alsophis* and is quite unlike that of *Dromicus* in which strong apical disks are present.

Taxonomy and Origin. As noted above, the two species of the *andreae* group exhibit osteological features characteristic of both *Alsophis* and *Dromicus*, though closer to the former. In most external characters they seem closer to *Dromicus*, but in the structure of the hemipenis they differ markedly from that group, being extremely close to *Alsophis*. Taken as a whole, this group cannot easily be referred to either genus. With regard to both skull and hemipenial characters, these two species resemble certain members of the South American genus *Lygophis*. The hemipenis in members of the latter genus, as currently recognized, is very heterogeneous. The organ may possess well-differentiated apical disks as in *L. lineatus* (Fig. 28A), the type species, and *L. flavifrenatus*, or it may be essentially of the *Alsophis* type, as in *L. boursieri* (Fig. 28B), in which the apical calyces are more spinulate along their margins than in the *Alsophis* type. Of these three species, *Lygophis boursieri* (Ecuador
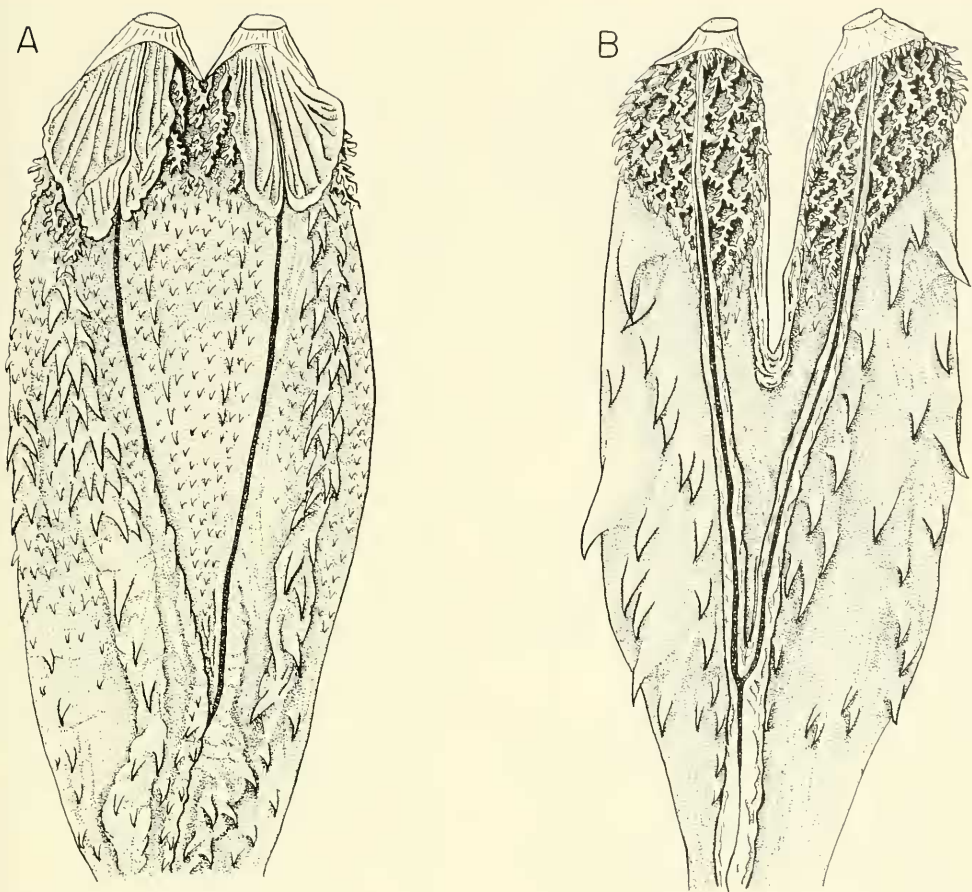
Fig. 28. Hemipenis morphology in the South American genus *Lygophis*; semidiagrammatic. The organ is uneverted and dissected *in situ*. A, *Lygophis lineatus*, MCZ 80994; B, *Lygophis boursieri*, MCZ 36948. Approx. × 5.

and Colombia) is very close to *andreae* and *parvifrons* in both skull and hemipenial characters, as well as in external scale pattern.

From this incomplete study of *Lygophis*, it seems possible that we may be dealing with a compound genus of distantly related forms. The evidence seems to suggest that *L. boursieri* might be placed in a separate genus with *andreae* and *parvifrons* as a specialized radiation, perhaps derived from mainland *Alsophis*; and that the type of *Lygophis*, *L. lineatus*, may need to be synonymized with *Dromicus* from which it differs primarily in the lack of

scale pits and the presence of basal hooks on the hemipenis (Roze, 1964). However, we must await more detailed taxonomic work to clarify these issues.[1] Nevertheless, it seems clear that generic distinctions between *Dromicus* (present concept) and

[1] In a reappraisal of South American snakes related to *Lygophis boursieri*, Myers (1969) established the *boursieri* species group including *Rhadinaea antioquiensis*, *R. tristriata*, and *L. boursieri*. The group is placed in *Lygophis* "... simply because *boursieri* already resides there." But the artificiality of the resulting genus is clearly pointed out, and the necessity of generic reassignment is affirmed.

Lygophis (see Roze, 1964) rest on slim evidence.

Since on present generic concepts it is not possible to accommodate the species of the *andreae* group in any existing genus, it seems best to propose a new generic name. Though close similarities exist between *andreae* and *parvifrons* and at least part of what is now called *Lygophis*, the type species, as stated above, is certainly distinct from them on the generic level. The solution adopted here, though not completely satisfactory, seems the most desirable one until a complete revision of the mainland forms is undertaken.

Antillophis nov. gen.

Type species: *Dromicus parvifrons* Cope 1862. Proc. Acad. Nat. Sci., Philadelphia, 1862, p. 79.

Distribution of genus: Hispaniola, Gonave Island, Vache Island, Tortue Island, Cuba, Isle of Pines.

Diagnosis: Small to medium-sized xenodontine snakes having generally long and narrow frontal bones as in *Alsophis*, but narrow prefrontal bones as in *Dromicus*; scale rows 17–19; 9–10 lower labials, 8 upper labials with nos. 3, 4, and 5 bordering the orbit as in *Alsophis*, but unlike *Dromicus* in which only nos. 3 and 4 generally border the orbit; one sensory pit on each dorsal body scale as usual in *Dromicus*, but unlike the usual condition in West Indian *Alsophis* or in *Lygophis*; hemipenis like that in *Alsophis*, lacking the apical disks of *Dromicus* and the disks and basal hooks of *Lygophis*.

Zoogeography. On present evidence it is not possible to determine the zoogeographic history of this assemblage, and it seems fruitless to indulge in speculation at this time. If, as suggested, *andreae* and *parvifrons* are derivatives of a mainland stock close to *L. boursieri*, then their entrance into the West Indies must have involved a colonization independent of that of *Alsophis*. It is possible, however, that further evidence will suggest a West Indian origin for these two species from the genus *Alsophis*.

FUNEREUS SPECIES ASSEMBLAGE

Included West Indian species: *callilaemus* Gosse, Jamaica; *dolichurum* Werner, Cuba; *funereus* Cope, Jamaica; *haetiana* Cochran, Hispaniola; *polylepis* Buden, Jamaica; *exiguus* Cope, Puerto Rico, Virgin Islands; *taeniatum* Günther, Cuba; *vittatum* Gundlach, Cuba.

Osteology. This group of eight species is very distinctive and is clearly separable from other West Indian xenodontines. They are all very small in size. The prefrontal bone is unlike that of *Alsophis* or *Dromicus* (Fig. 5). It is moderately long dorsoventrally, narrow and gently curving with nearly parallel anterior and posterior edges. The two frontal bones together form a square plate above the orbits, unlike the condition in other West Indian groups. Ventrally the parasphenoid is proportionately wider along its entire length, especially posteriorly. The skull is proportionately flatter, and thus the interorbital partition formed by the dorsal extension of the parasphenoid does not extend above the trabecular grooves. Rather, the frontal bone on each side covers the entire lateral aspect of the parasphenoid. The supratemporal and quadrate are reduced in size, and the latter is flat and triangular in shape.

On Jamaica there are three species of this group, *funereus*, *polylepis*, and *callilaemus*. The specific distinction between *funereus* and *polylepis* has recently been demonstrated by Buden (1966), but osteologically they are very similar. They have the highest dental formulae of the group (Fig. 29) with about 19 + 2 maxillary, 11 palatine, 19 pterygoid, and 24 dentary teeth in *funereus*, and 17 + 2 maxillary, 11 palatine, 24 pterygoid, and 27 dentary teeth in *polylepis*. The parasphenoid bone beneath the orbits is broad throughout its

Fig. 29. Observed ranges of variation in numbers of teeth on each tooth-bearing element for the eight species of the *funereus* species assemblage.

length, being wider anteriorly, and bears a deep midventral groove along its entire length (Fig. 30). The postorbital bone is short and stout and is separated from the frontal only by a small spur of the parietal. The juxtastapedial fossa leading to the fenestra ovalis is variable in the degree of closure around the columella; it may be widely open and rounded, formed equally by the prootic and exoccipital bones as in most other West Indian xenodontines (Fig. 31A), or it may be constricted dorsoventrally by a ventral extension of the prootic portion of the fossa.

Also on Jamaica is the species *callilaemus* which is clearly related to *funereus*. The premaxilla and nasal are more solid and compact. The supratemporal and quadrate are further reduced, but this is probably a result of the smaller size of this species. The juxtastapedial fossa tends to be even more constricted than in *funereus*, and it may be nearly divided into two separate openings (Fig. 31B). The columella extends out of the posterior opening and is directed more posteriorly than laterally. The parasphenoid is wider than in *funererus*, and the midventral groove is
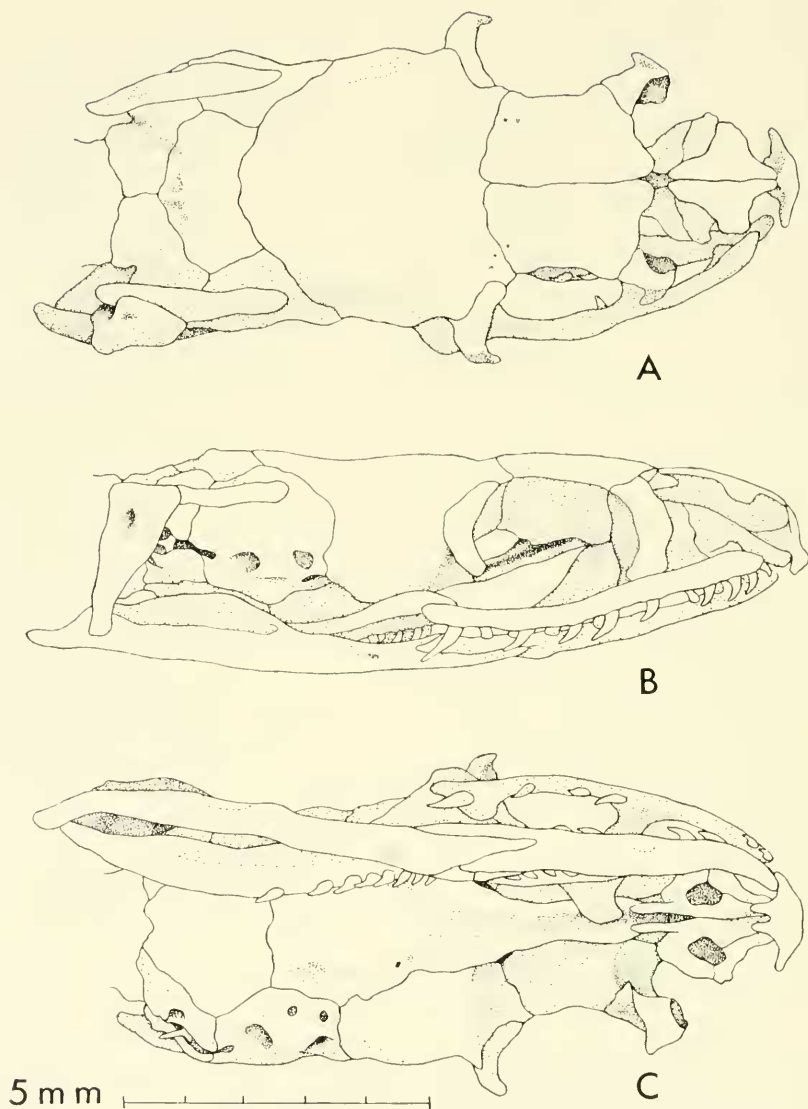
Fig. 30. Skull structure in *Arrhyton funereus*, MCZ 44901. A, dorsal view; B, lateral view; C, ventral view.

more conspicuous. The dental formula is lower with about $12 + 2$ maxillary, 7 palatine, 16 pterygoid, and 18 dentary teeth.

At least three species found on Cuba may be referred to this assemblage. Of these *vittatum* is closest to *callilaemus*. The dentition is not strikingly different; there are approximately $14 + 2$ maxillary, 12 palatine, 10 pterygoid, and 16 dentary teeth. The parasphenoid is variable in width as is the degree of closure of the juxtastapedial fossa. The premaxilla and nasal are massive elements which approach the type found in some burrowing forms. The orbit is small, and the postorbital bone is slender and in contact with the frontal bone; there is no intervening parietal spur. The supratemporal and quadrate are even

more reduced than in the Jamaican form. The otic region is expanded so that it is the widest part of the brain case. The subspecies *vittatum landoi* is like *vittatum vittatum* in skull structure, but the dentition is somewhat reduced; there are about 11 + 2 maxillary, 9 palatine, 9 pterygoid, and 14 dentary teeth.

In another Cuban species, *dolichurum*, the parasphenoid bone is even broader than in *vittatum* and the premaxilla is more robust. The supratemporal is reduced to a mere splint, and further reduction in the postorbital bone is evident. In its dental formula *dolichurum* shows a reduction over *vittatum landoi* and has about 10 + 2 maxillary, 7 palatine, 6 pterygoid, and 12 dentary teeth.

It is in *taeniatum* (Cuba) that we find the greatest development of the trends observed in the series leading from *funereus* and *callilaemus* on Jamaica to *vittatum* and *dolichurum* on Cuba. The parasphenoid is very broad with a very wide but shallow midventral groove. The skull (Fig. 32) is proportionately longer than in *dolichurum*, and the orbit is relatively smaller (see Fig. 33). Reduction of the supratemporal is not quite so great as in that species. The nasal is an elongated solid bone, and the premaxilla is massive and in firm contact with the nasals. The dental formula is the lowest of the entire assemblage with approximately 6 + 2 maxillary, 5 palatine, 8 pterygoid, and 10 dentary teeth. The constriction of the juxtastapedial fossa is complete; bony dorsal and ventral growths from the prootic and exoccipital bones close off the center of the fossa, leaving two openings to the outside. The columella extends nearly straight backwards out of the posterior opening, and the newly formed anterior opening lies close to the foramen for the mandibular nerve (Fig. 31C).

The Hispaniolan species of this assemblage is *haetiana*, a montane form somewhat differentiated externally, but osteologically close to the other members of the group. The shape of the frontal bone is the same
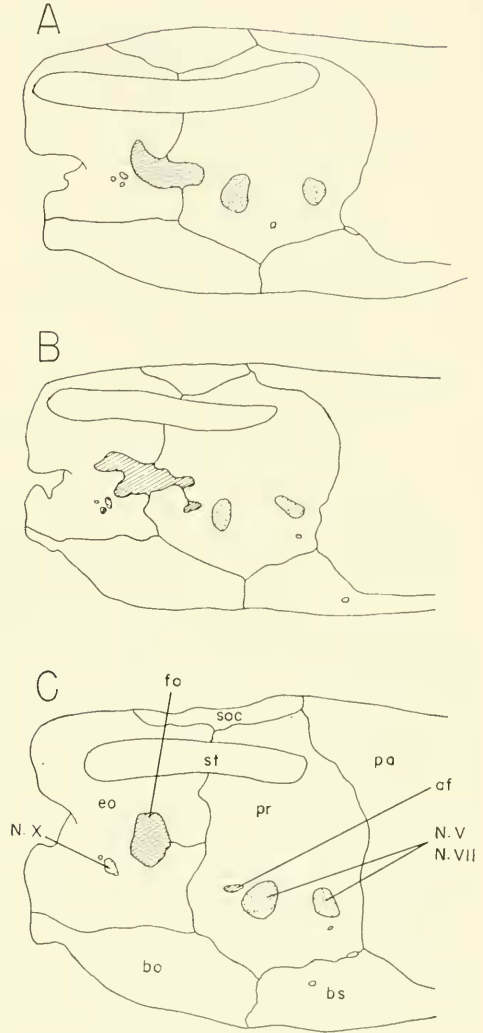

Fig. 31. Variation in the structure of the juxtastapedial fossa and foramen ovalis in the *funereus* species assemblage. A, *Arrhyton funereus*, MCZ 13294; B, *A. callilaemus*, MCZ 69078; C, *A. taeniatum*, MCZ 19874. Roman numerals, foramina for cranial nerves. Abbreviations: af, "anterior foramen," see text; fo, foramen ovalis. Other abbreviations as in Fig. 2. Approx. × 12.

as in *funereus* (Jamaica), and the prefrontal and postorbital are similar. As in the latter, the parietal spur between the frontal and postorbital is very small. In the degree of reduction in the supratemporal and quadrate, and in general skull
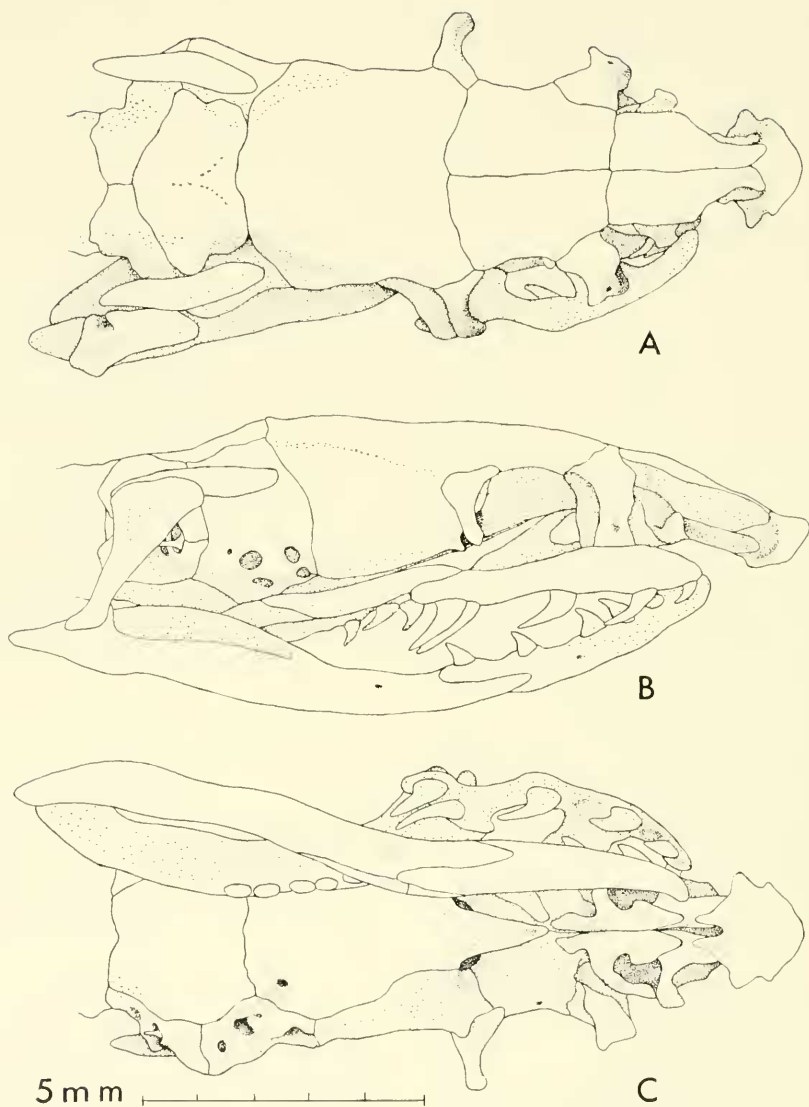
Fig. 32.   Skull structure of *Arrhyton taeniotum*, MCZ 44901.   A, dorsal view; B, lateral view; C, ventral view.

proportions, *haetiana* is similar to *funereus*. The orbits are reduced in size nearly as much as in *taeniatum*. The otic region is expanded as in the Jamaican species and the juxtastapedial fossa varies from widely open to completely closed. In *haetiana* may be seen the beginning of a trend in a direction opposite from that seen in the *callilaemus-taeniatum* series. Here the para-sphenoid is narrower than in *funereus*, and the dental formula is unreduced, with about 17 + 2 maxillary, 11 palatine, 24 pterygoid, and 22 dentary teeth.

The Puerto Rican species, *exiguus stahli*, is considerably larger than *haetiana*. The skull is proportionately narrower and as a consequence the frontals are relatively longer. The orbits are small as in other
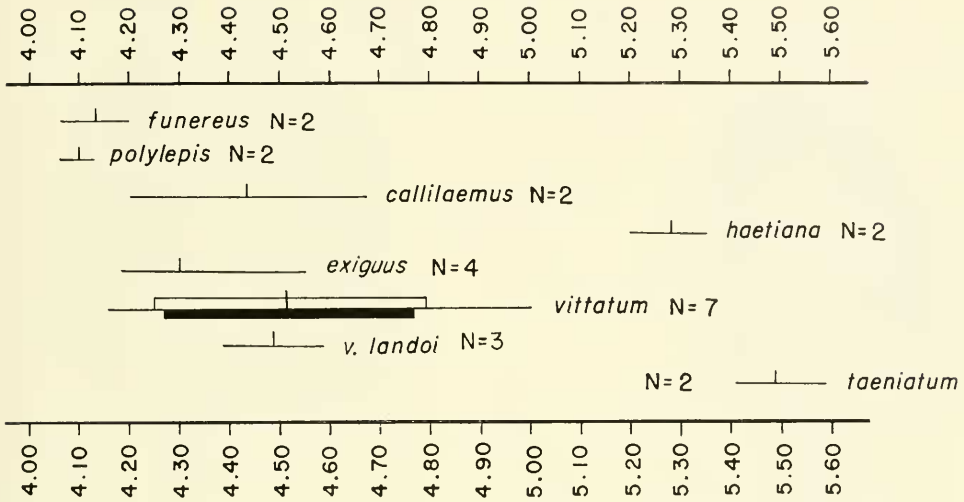
Fig. 33. Skull length/orbit length indices for seven of the eight species of the *funereus* species assemblage (*Arrhyton dolichurum* is not included). Horizontal line, observed range; vertical line, mean; open rectangle, ± one standard deviation from the mean; solid rectangle, 95 per cent confidence interval of the mean.

members of the group, but not as small relatively as in *haetiana*. The parasphenoid is as wide as in the Hispaniolan species. The dental formula is approximately 15 + 2 maxillary, 9 palatine, 23 pterygoid, and 22 dentary teeth, and is nearly the same as in *haetiana*. On the Virgin Islands the subspecies *exiguus exiguus* is very similar to *exiguus stahli* in osteological characters except for the lower dental formula (about 13 + 2 maxillary, 7 palatine, 17 pterygoid, and 19 dentary teeth), and the more reduced supratemporal. The species *exiguus* is superficially similar to *Dromicus juliae* (Dominica); the latter is small with a wide skull, short frontals, and reduced supratemporals. However, several important differences suggest that *exiguus* is not closely related to *Dromicus*, but that it is allied with the *funereus* assemblage. In *juliae* the parasphenoid is narrow and the interorbital partition is very prominent, as in *Dromicus*. The prefrontal is of the *Dromicus* type and is unlike that of *exiguus*. The orbit is large and the quadrate is relatively long. In all of these characters *D. juliae* contrasts with *exiguus*.

On these grounds (and on external and hemipenial evidence), *exiguus* is placed in the *funereus* group close to *haetiana*.

External morphology. Externally the *funereus* species group is more diverse than the three other West Indian groups discussed above. The usual number of supralabials is seven, but may be seven or eight in *haetiana* and six or seven in *dolichurum*. In *exiguus* the usual number is eight. The infralabials number eight in the Jamaican species (*funereus, polylepis,* and *callilaemus*), eight or nine in the Cuban forms (*taeniatum, vittatum,* and *dolichurum*), usually eight and more rarely nine in *haetiana*, and nine in *exiguus*. The number of scale rows is 17 in all of the Cuban species and 19 in the remainder of the group. Ventral scale number may vary from a median of about 118 in *vittatum* to about 181 in *taeniatum*; caudal counts vary from a median of about 45 in *haetiana* to one of about 119 in *dolichurum*. The loreal is absent in *haetiana* and *taeniatum*, but the method of scale loss in the two species was different. In *taeniatum* the prefrontal scale has either extended downward later-
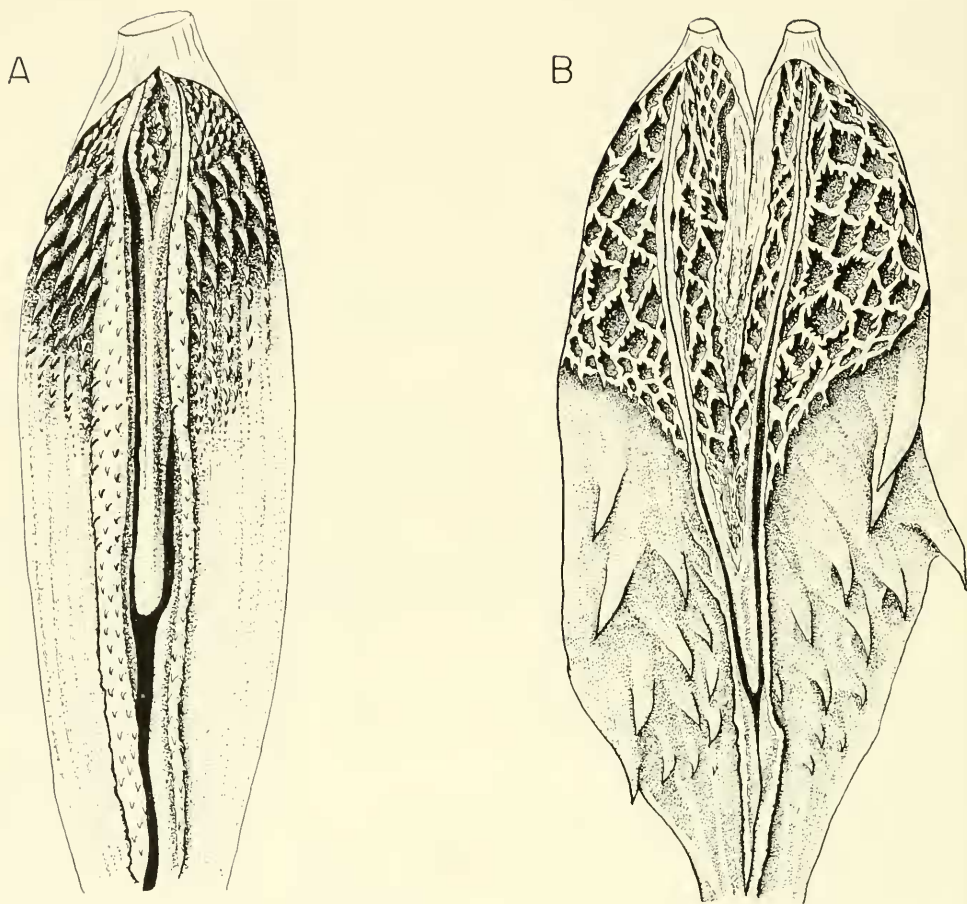
Fig. 34. Hemipenis morphology in the *funereus* species assemblage; semidiagrammatic. The organ is uneverted and dissected *in situ*. A, *Arrhyton funereus*, MCZ 13295; B, *A. vittatum*, MCZ 42505. Approx. × 5.

ally to take the place of the loreal and thus lies between the nasal and the preocular, or else the loreal has fused with the frontal, giving the same result. In *haetiana* the nasal has either replaced the loreal by being extended backward to contact the preocular, or has fused with the loreal.

Of the diagnostic characters used by Cochran (1941) in her description of *Darlingtonia haetiana*, only two set this species apart from the other members of the present species assemblage. These are: the single anal plate in contrast to the divided plate of the other species; and the first pair of lower labials not meeting in the midventral line. In view of the scale variations already noted for this group, these characters are only doubtfully of generic value in this assemblage.

With respect to scale pits, *funereus* and *polylepis* have two pits per dorsal body scale, *callilaemus* has only one. The pit in the latter is asymmetrical and suggests its derivation from a two-pit condition by the loss of one pit. The Cuban species lack scale pits, as does *haetiana*. On Puerto Rico *exiguus stahli* has no pits on most of the body scales, but may have two pits on the scales of the dorsal side of the neck. The subspecies *exiguus exiguus* has no

pits. In view of the numerous other characters indicating close relationship, scale pits do not appear to be reliable as a taxonomic character above the species level in this group of snakes. Roze (1958) came to the same conclusion with reference to "Urotheca," and I have suggested the same for *Alsophis*, above.

Hemipenis. As seems to be the case with other characters, the structure of the hemipenis is considerably more variable here than in other West Indian groups. In *funereus* and *polylepis* the organ is undivided although the sulcus spermaticus is deeply forked (Fig. 34A). Small spines are situated along the sulcus from the base to somewhat beyond the point of branching, whereupon lateral bands of spines encircle the organ. In *funereus*, spinose folds of tissue border the sulcus for much of its length, and fine spinose papillae cover the apex. In *callilaemus*, the hemipenis is weakly bifurcated and bears several rows of relatively large spines along the sides of the sulcus. These grade into fine spines basally. The apex of each lobe is covered with soft spinose calyces. The hemipenis in *taeniatum* and *vittatum* (Fig. 34B) is of the *callilaemus* type, but the lateral spines extend further towards the apex; the latter is covered with calyces of fine papillae instead of soft spines. This distinction, however, is very slight and the two forms are essentially the same. In *haetiana* the organ is essentially like that of *callilaemus*, but as in the Cuban species the spines extend more distally, and the apical ornament consists of papillate calyces. The Puerto Rican and Virgin Island species *exiguus* has a more deeply bifurcated hemipenis than does *haetiana*, and the area of strongly reticulated apical papillae is sharply demarcated around its edge.

Figure 35 summarizes the geographic distribution of some of the more important morphological characters.

Origin. The *funereus* species assemblage cannot easily be derived from any other

West Indian group. Turning to the mainland, the genus *Rhadinaea*[1] shows a remarkable similarity to the *funereus* group as a whole.[2]

The external scale pattern in species of *Rhadinaea* shows a variation equal to that of the *funereus* group. The supralabials are usually eight in number, except in *R. flavilata* and *R. calligaster* in which there are seven. The number of infralabials may be eight, nine, or ten. The fifth infralabial is the largest of the series in the *funereus* group, but in *Rhadinaea* the largest may be the fourth, fifth, or sixth scale. Considerable variation is seen in the structure of the hemipenis also. In most species of *Rhadinaea*, such as *R. flavilata* and *R. decorata*, the organ is not bifurcated and the sulcus spermaticus is only very weakly divided near the apex. Very large lateral spines are arranged in several rows along the sides of the sulcus. The apex is capitate with spinulate calyces arranged in several thick folds. In *R. calligaster* the sulcus is more deeply divided. The apex is only weakly capitate and the thick folds are lacking; the hemipenis is similar to that of *vittatum* (Cuba), with papillate calyces rather than spinulate ones.

In its osteology *Rhadinaea* is basically like the *funereus* group. The shape of the prefrontal bone is distinct from the Antillean forms for the most part; the ventral half is greatly constricted anteroposteriorly. However, this is variable and in some species this bone approaches the condition found in the *funereus* assemblage. The skull is short and the supratemporal bone is reduced. In some forms, such as *R.*

[1] This generic name is used here in the sense of Myers (1967) and is considered equivalent to *Urotheca sensu* Roze (1958).

[2] *Rhadinaea dumerillii*, the type species, was unavailable for study, but from Bibron's (1843) figure and description it appears to be close to Central American species of *Rhadinaea* and unlike any Cuban species. *R. dumerillii* now appears not to be a Cuban form as originally described, but almost certainly a mainland form (Roze, 1958).
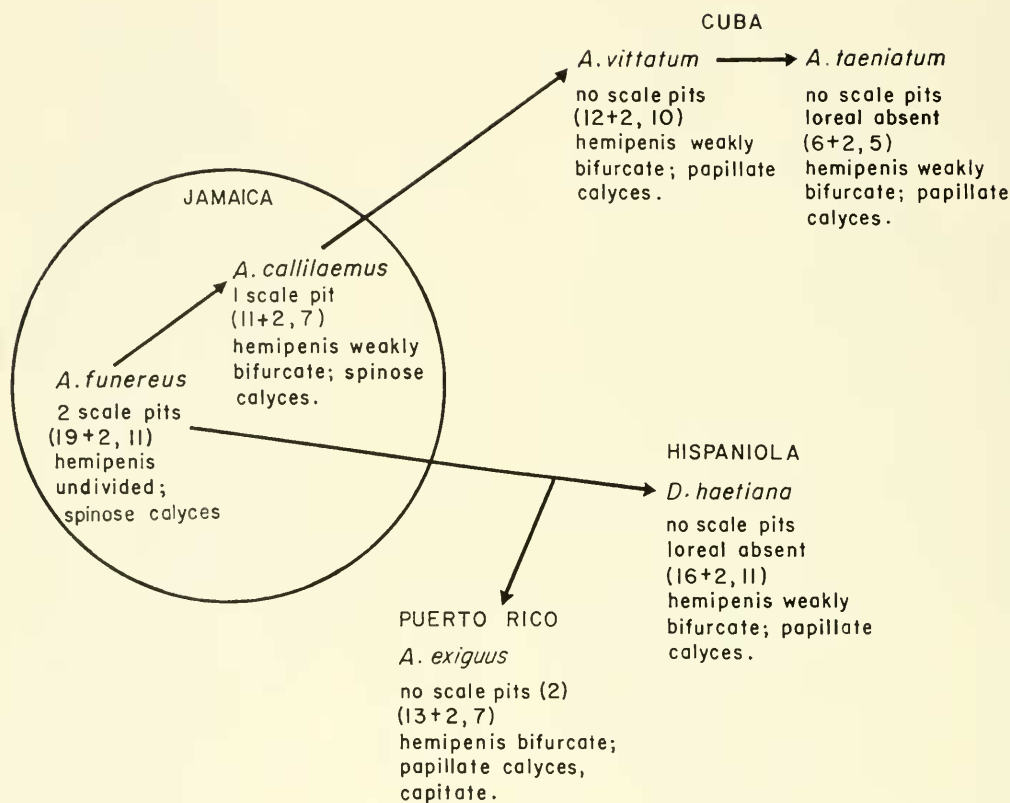
Fig. 35. Geographic distribution of several morphological characters in the *funereus* species assemblage. The circle represents the supposed center of dispersion for this group.

decorata, the parietal spur between the frontal and the postorbital is short as in *funereus*. In *R. serperaster* and *R. lateristriga* the parasphenoid bone is very wide and bears a deep midventral groove. All of the characters that distinguish the *funereus* assemblage from other West Indian xenodontines also occur within *Rhadinaea*, although no one of the species examined possesses all of these characters. Although it seems likely that no one living species of *Rhadinaea* can now be considered as the ancestor of the West Indian *funereus* group, it is not unreasonable to suggest a common descent for both groups from an ancestral form combining the requisite characters, all of which occur in various combinations throughout this morphologically broad genus as presently defined.

It is, of course, possible that the morphological similarities between *Rhadinaea* and the *funereus* group are the result of habitus rather than heritage characters, and that both groups have evolved in parallel fashion with respect to those characters related to a semiburrowing mode of life. There appear to be certain features common to most semiburrowing xenodontines, and these almost certainly evolved independently in many groups under the influence of similar habitus selection. But the exact way in which parallel characters are achieved, even under identical selection

pressures, depends upon raw materials in the form of existing morphological structures, and upon genetic variability. The more distantly related any two forms are, the more likely it is that they will achieve functionally similar adaptations in a divergent way.

An examination of semiburrowing adaptations in xenodontine snakes of the New World shows similar osteological trends common to all of them, but, as expected, they differ from each other in details. In most osteological characters studied, *Rhadinaea* and the *funereus* group exhibit a similarity of form which suggests more than morphological parallelism with respect to semiburrowing adaptations.

The osteological modifications which generally appear to be associated with semiburrowing adaptations are: small body size; reduction in relative orbit size; shortening of the parietal region of the skull; enlargement and consolidation of the preorbital bones to form firm contacts with each other; broadening of the parasphenoid bone associated with the reduced orbits; relative broadening of the otic region so that it becomes the widest part of the skull (probably associated with general streamlining); reduction of the supratemporal and quadrate bones; and, a relatively low number of teeth.

With respect to all of these characters, as well as others not obviously correlated with burrowing, the *funereus* group and *Rhadinaea* show a close correspondence, differing only in the structure of the prefrontal bone. The frontal bones form a nearly square plate above the orbits and contact the parietals in a broad, nearly straight suture. In contrast, the parietals of *Geophis mutitorquis* extend lateral to the posterior half of the frontals, occupying a deep groove in the latter. A similar condition exists in *Apostolepis ambinigra*, where the frontals are trapezoidal in shape, being wider anteriorly. In *Atractus latifrons* the frontals are oval in shape, with their long axis in the transverse direction.

In the *funereus* group and *Rhadinaea* the parietal retains the shape normal for nonburrowing xenodontines. In *Geophis mutitorquis* a posterior process extends into the deeply divided interparietal, and in *Atractus latifrons* and *Rhinostoma guianense* the parietals are so shortened that they are broader than long.

The reduced quadrate in the *funereus* group and *Rhadinaea* is thin and triangular in shape. In *Rhinostoma guianense* and *Drepanoides eatoni* the quadrate retains its normal rodlike shape. It should be emphasized that in xenodontine snakes generally, the quadrate and supratemporal appear to increase allometrically with body size and, therefore, the reduced size of these elements in most semiburrowing forms may, in part, be the result of their small size.

The *funereus* group and *Rhadinaea* have retained more or less normal skull proportions, except for *A. taeniatum* in which the skull is somewhat elongated. In *Rhinostoma guianense* the skull is much shortened, whereas in *Apostolepis ambinigra* it is greatly elongated.

In the *funereus* group and in *Rhadinaea* only *taeniatum* shows some enlargement of the nasals and premaxilla and a definite trend towards consolidation of the preorbital region of the skull. In *Carphophis amoena* and *Apostolepis ambinigra* the nasals are greatly enlarged and form a firm contact with the frontals and premaxilla.

In general skull details, *Rhadinaea* and the *funereus* group approximate each other in numerous ways and contrast with most other semiburrowing xenodontines from the mainland, although they show a closer resemblance to forms like *Drepanoides* than to others like *Rhinostoma*, *Apostolepis*, and *Carphophis*. The close similarity between *Rhadinaea* and the *funereus* group in osteological and other characters (excepting the hemipenis) suggests a phylogenetic relationship rather than morphological convergence, though additional evidence is needed. The differences in the

hemipenis between these two groups rests primarily in the capitation of the organ in *Rhadinaea* and the lack of capitation in the *funereus* assemblage. I do not, however, feel that this difference is so significant as to preclude their belonging to a phylogenetically related group of genera.

It was stated above that *vittatum landoi* was distinct from *vittatum vittatum* in its dentition. In this respect *v. landoi* is intermediate between *vittatum vittatum* and *dolichurum*. Schwartz (1965) discussed the differences in ventral and subcaudal scale count and body length between the two subspecies of *vittatum*. These characters, together with the clear difference in dentition, indicate a distinction worthy of specific recognition, and the taxon *landoi* should probably be raised to the rank of full species. However, since the present sample of *v. landoi* was too small (three specimens) to determine the degree of variation, it is here, for the present, retained as a subspecies of *vittatum*.[1]

Despite the morphological variation within the *funereus* group, it is difficult to divide these species into distinct genera. Although usually placed in different genera, *vittatum* (Cuba) is closer to *callilaemus* (Jamaica) in dentition, osteology, and external scale pattern than it is to *taeniatum*. Both *vittatum* and *callilaemus* form intermediate grades between *funereus* and *taeniatum*, and a generic boundary within this group cannot be distinguished adequately. As discussed above, *exiguus* (Puerto Rico) shows certain similarities to species of the genus *Dromicus*. However, its totality of characters, especially the hemipenis, makes a close relationship between the two unlikely. On present evidence *exiguus* seems allied to the present assemblage. The three species, *funereus*, *haetiana*, and *exiguus*, form a morphological series distinct from that leading to

taeniatum, although *haetiana* appears to have diverged from both *funereus* and *exiguus* in certain external characters. These characters have been used to separate *haetiana* from other West Indian species on the generic level (see above). It is my feeling that generic splitting within the present species assemblage will obscure the clear relationships between all of these species which (except possibly for *exiguus*) certainly represent a phylogenetically related group. However, constancy in classification makes the retention of the genus *Darlingtonia* for *haetiana* desirable at this time.

The exact phyletic relationships between *exiguus* and other West Indian species is, as indicated above, not completely certain. Although open to question, I feel that this species could be considered congeneric with the *funereus* group without unduly broadening the limits of that assemblage.

Although the morphological similarities between the genus *Rhadinaea* and the *funereus* assemblage possibly suggest an ancestor-descendant relationship (or perhaps a more distant common ancestry), the *funereus* group is generically distinct from *Rhadinaea* on present evidence. The *funereus* assemblage, then, should be referred to the genus *Arrhyton*, which has priority, and the type species, unfortunately, is *A. taeniatum*, the most specialized form. The proposed phyletic relationships between *Rhadinaea* and the species of the genus *Arrhyton* are summarized in Figure 36.

Zoogeography. In terms of species diversity the center of distribution of *Rhadinaea* today is Central America. Beginning from a closely related stock, we may suggest the following zoogeographic history for this group. From an early stock of this (or an ancestral) genus a single oversea colonization presumably resulted in the establishment of the *Arrhyton funereus* prototype on Jamaica. *Arrhyton polylepis* is extremely close to *A. funereus* and the two forms appear to be relatively

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[1] After the present paper was sent to press, Lando and Williams (1970) formally raised *landoi* to the rank of full species.
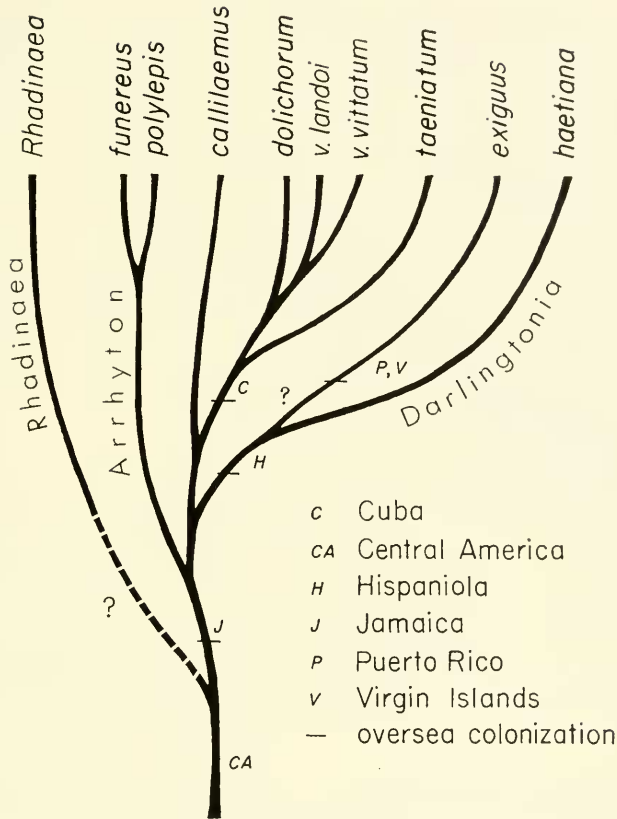
Fig. 36. Suggested phyletic relationships between the species of the *funereus* species assemblage and the genus *Rhadinaea*. Short horizontal lines indicate proposed oversea colonizations.

recent products of speciation on that island. The most primitive member of the genus is *A. funereus* which forms the base of both the *A. funereus–A. taeniatum* series and the *A. funereus–A. exiguus* series. It is the only Antillean species (except for *A. polylepis*) with a nonbifurcated hemipenis and in this respect is closest to species of *Rhadinaea*. Within the *A. funereus–A. taeniatum* series it is the least specialized in terms of the reduction of skull bones and other semi-burrowing adaptations. From this early *A. funereus* stock two basic lines appear to have been established; *A. callilaemus* (Jamaica) began a trend toward reduction of the posterior skull bones and in the dentition, and a widening of the para-

sphenoid bone. A colonization of Cuba from this early *A. callilaemus* stock led to the Cuban forms which, through repeated speciation, continued the trend, with *A. taeniatum* as the most highly specialized species of the group. The second line resulted from a migration to Hispaniola and tended toward a narrower parasphenoid, larger size, and in many ways a general convergence toward other West Indian xenodontine groups, especially *Dromicus*. This may have been related to a general tendency away from semiburrowing adaptations. In order to derive *A. exiguus* from this early Hispaniolan form we must postulate a widespread distribution for this latter form before (or concurrent with) its differ-
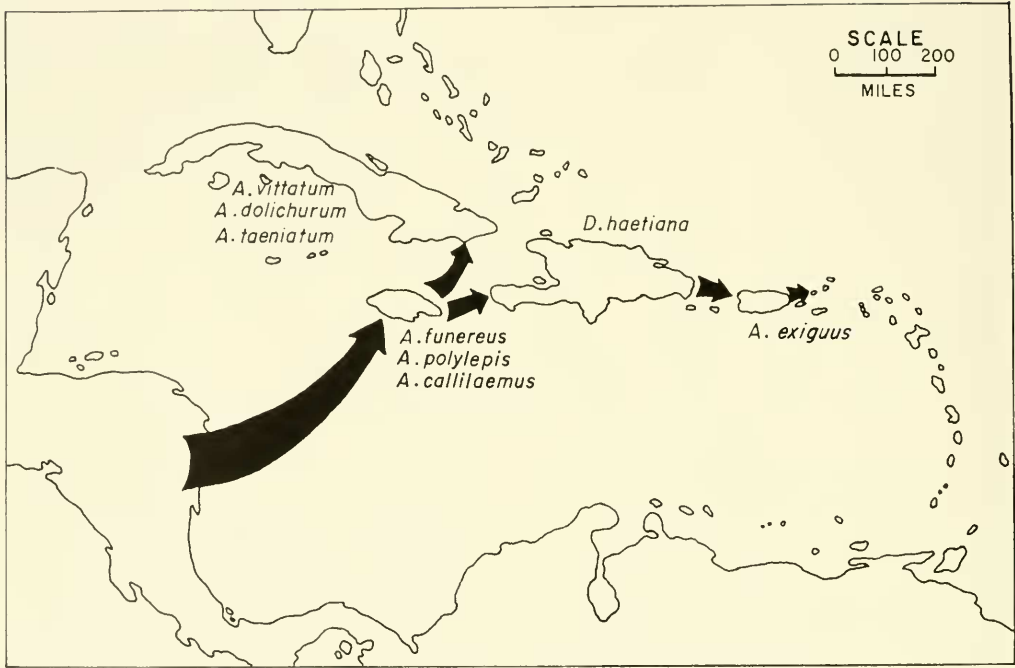
Fig. 37. Proposed routes of colonization of the West Indies by the *funereus* species assemblage. The arrows are not intended to represent exact paths. The distribution of extant species is as indicated.

entiation into the morphologically somewhat specialized and ecologically restricted species *Darlingtonia haetiana*. Today *D. haetiana* occurs only in the montane massifs of the southwestern and Barahona peninsulas at altitudes ranging from 1000 to 5600 feet. One possible explanation for the peculiar distribution of this species is an ecological replacement of the former widespread species (possibly by *parvifrons?*) with *D. haetiana* remaining as a montane relict. This zoogeographic pattern is summarized in Figure 37.

A PROBLEMATICAL GENUS

Two species remain to be discussed: *Ialtris dorsalis* and *I. parishi* from Hispaniola. *Ialtris dorsalis* (I have not seen *I. parishi*) is a large species and is most similar to *Alsophis* in many skull characters, but distinct in many external and hemipenial characters. The skull is narrower, especially in the otic region. In its dentition this species is unique among West Indian xenodontines in having prominent grooves on the enlarged posterior maxillary teeth. The bilobed hemipenis is very long, ridged with numerous folds, and has an apical ornament of weakly developed flounces. Externally there are seven upper labials as in *Arrhyton* generally, but the ventral and subcaudal scale counts are similar to those of *Alsophis*. *Ialtris dorsalis* (and presumably *I. parishi* also) is not very close to any other Antillean species as far as can be determined from its present morphological specializations and therefore certainly should be retained in a distinct genus. In most characters *Ialtris* shows its greatest similarity to *Alsophis*, and it may have been derived from that genus on Hispaniola.

CONCLUSIONS

The use of skull and hemipenial characters, in addition to those of external

TABLE 2

Distinguishing characteristics of the eight genera of xenodontine colubrid snakes in the West Indies as discussed in the text.

Genus	prefrontal	frontal	hemipenis	size	supra-labials	grooved max. teeth	anal scale	no. sensory pits	loreal scale
Alsophis	cantherigerus type	long and narrow	no disk	large	8	no	divided	2(1)	present
Dromicus	melanotus type	short and narrow	apical disk	medium	8	no	divided	1(0)	present
Antillophis	melanotus type	long and narrow	no disk	medium	8	no	divided	1	present
Arrhyton	funereus type	square	no disk	small	7–8	no	divided	0–1	present (absent in A. taeniatum)
Darlingtonia	funereus type	square	no disk	small	7–8	no	complete	0	absent
Hypsirhynchus	cantherigerus type	long and narrow	no disk	large	8	no	divided	1	present
Uromacer	cantherigerus type	long and narrow	no disk	large, arboreal	8	no	divided	0	present
Ialtris	cantherigerus type	long and narrow	no disk	large	7	yes	divided	0	present

morphology, appears to be of significant aid in suggesting relationships between species of West Indian xenodontine colubrid snakes. They not only provide data for a proposed redefinition of generic concepts, but suggest certain phylogenetic relationships with mainland groups. Such relationships are of considerable interest, since they allow a tentative reconstruction of the possible origin and history of these snakes in the Antilles. The generic groups of xenodontine snakes here recognized in the West Indies and listed in Table 1 may be distinguished as in Table 2.

The present xenodontine fauna of the West Indies was possibly wholly derived from Central and South American stocks through at least four oversea colonizations. Based on present evidence, a summary of the postulated historical events follows: 1) From the formerly widespread South American genus *Alsophis,* a waif colonization established this group on Cuba. Sub-

sequent radiation into a number of species and endemic genera led to its present distribution throughout the Greater Antilles and the northern Lesser Antilles. A minimum of three separate inter-island migrations of this group is required to explain the peculiar faunal assemblage of Hispaniola. 2) The specialized genus *Ialtris* possibly emerged from *Alsophis* on Hispaniola. 3) Using Jamaica as a port of entry and center of dispersion, a single stock, possibly derived from the Central American genus *Rhadinaea,* successfully spread through the Greater Antilles in two distinct but closely related lines and established the genera *Arrhyton* and *Darlingtonia.* 4) Possibly derived from part of what is now called *Lygophis* in South America, the species *andreae* and *parvifrons* may have reached Cuba and Hispaniola by a direct oversea colonization. 5) A relatively recent invasion of the Lesser Antilles by a species of *Dromicus* (= *Leimadophis*) almost cer-

tainly entered via Trinidad, but has not yet progressed beyond Guadeloupe.

The chronological sequence of colonizations cannot definitely be established on present evidence. However, a sequence roughly similar to that above is not unreasonable. It, of course, cannot be assumed that the West Indies were devoid of a xenodontine ophifauna before the series of colonizations that established the present fauna, but our knowledge of earlier xenodontine colonizers is nonexistent because of the lack of a significant fossil record.

From the patterns of dispersion discussed in this paper it would appear that numerous combinations of inter-island migrations have occurred. The main sequences have progressed from one island to the next adjacent island and in this sense were for the most part linear. The following series have been proposed: mainland-Cuba-Hispaniola-Puerto Rico-Lesser Antilles; mainland-Cuba-Jamaica-Hispaniola; mainland-Cuba-Bahamas; mainland-Jamaica-Cuba; mainland-Jamaica-Hispaniola-Puerto Rico; mainland-Trinidad-Lesser Antilles.

Inter-island migration, especially to centrally located Hispaniola, seems to have been more frequent than mainland-island migrations. This was certainly the result of the greater cross-water distance between the mainland and any island than between the various islands themselves, as Simpson (1956) and Darlington (1957) have suggested. The greatest diversity in species and genera occurs on Hispaniola; this is to be expected in view of its central position and consequently greater number of colonizations. Its large size, varied habitats, complex physiography and history have provided an excellent opportunity for immigrants to differentiate into noncompeting forms.

The zoogeographical patterns here proposed are based on limited evidence and are in large measure speculative. It is hoped that they offer a workable contribution toward the continued study of this group. However, only when adequate information about the comparative anatomy, karyotypes, ecology, physiology, and biochemistry of all Antillean snakes and their mainland relatives is available will we be able to draw firmer conclusions concerning the origin and zoogeography of xenodontine snakes in the West Indies.

ACKNOWLEDGMENTS

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APPENDIX

DENTAL FORMULAE AND VARIATION FOR WEST INDIAN AND SOME RELATED MAINLAND AND GALAPAGOS XENODONTINE COLUBRID SNAKES. VARIATION INCLUDES RANGES OF SUBSPECIES.[1]

	N^2	maxillary	palatine	pterygoid	dentary
Alsophis					
angustilineatus	1	$11+2$	11	17	18
anomalus	1	$12+2$	8–9	20	18–19
antillensis	6	$16–19+2$	11–13	28–30	24–26
ater	4	$16+2$	13–16	26–27	22–25
biserialis	1	$12+2$	7	16	17
cantherigerus	12	$11–15+2$	9–12	23–30	17–21
chamissonis	2	$9+2$	7–8	10–14	15–16
dorsalis	1	$12+2$	7	16	17
melanichnus	1	$18+2$	16	28	24
portoricensis	10	$14–18+2$	9–12	26–32	23–35
rijgersmai	2	$16–17+2$	11–13	26–30	23–24
rufiventris	3	$16–18+2$	11–15	25–28	21–26
sancticrucis	2	$17–19+2$	12–13	30–32	22–23
stevini	1	$11+2$	8	18	19
tachymenoides	1	$11+2$	10	16	21
vudii vudii	4	$11–13+2$	9–10	20–27	19–23
vudii utowanae	2	$15+2$	12–13	29–31	22–23
Antillophis gen. nov.					
andreae	4	$18–21+2$	15–16	34–35	25–28
parvifrons	13	$13–16+2$	10–13	25–27	19–24
Arrhyton					
callilaemus	2	$11–12+2$	7	16	18
dolichurum	1	$10+2$	7	16	12
exiguus	4	$13–16+2$	7–11	17–27	19–23
funereus	2	$19+2$	11	19	24
polylepis	2	$17+2$	11	23–24	26–27
taeniatum	2	$6+2$	5	7–8	10
vittatum vittatum	7	$12–15+2$	10–14	9–10	15–17
vittatum landoi	3	$10–11+2$	9	9	14–15
Conophis					
lineatus	1	$10+2$	7	17–18	18
Darlingtonia					
haetiana	3	$16–17+2$	11	22–25	20–24
Dromicus					
almadensis	2	$18–19+2$	15–16	27–28	26–29
amazonicus	1	$18+2$	12	22	23
bimaculatus	1	$21+2$	14	28	26
cursor	2	$20–21+2$	14–15	27–28	26
epinephalus	2	$22–24+2$	16–18	27–32	32
juliae	4	$24–26+2$	29–33	30–34	33–34
melanotus	3	$15–16+2$	10–11	23–26	16–22
ornatus	2	$19–20$	13	26	24–27
perfuscus	2	$15–16+2$	12–13	20–22	18–19
pseudocobella	1	$18+2$	13	23	19
reginae	1	$16+2$	12	27	20
taeniurus	1	$19+2$	11	25	25
Hypsirhynchus					
ferox	3	$11–12+2$	7	17–19	19–20

Appendix (Continued)

	N[2]	maxillary	palatine	pterygoid	dentary
Ialtris					
dorsalis	2	16+2	7	21	20
Liophis					
anomala	1	12+2	10	19	17
cobella	3	19–20+2	13–14	26–29	24–30
jaegeri	1	21+2	18	27	—
merremi	1	18+2	14	26	22
Lygophis					
boursieri	1	22+2	14	28	25
flavifrenatus	1	26+2	23	35	35
lineatus	2	19–20+2	14–15	29–32	27–29
Philodryas					
aestivus	1	14+2	11	20	19
burmeisteri	1	12+2	9	16	19
olfersii	1	10+2	9	17	13–14
Uromacer					
catesbyi	7	15–18+2	10–11	24–25	22–28
dorsalis	2	13–14+2	9	18	20–22
frenatus	4	14–16+2	9	18–19	24
oxyrhynchus	7	15–17+2	8–10	17–21	22–28
Rhadinaea					
brevirostris	1	14+2	9	21	18
decorata	1	22+2	14	34 ·	24
flavilata	1	24+2	11	24	20
serperaster	1	17+2	9	14–16	14

[1] Problematical subspecies which may be full species are listed separately.
[2] Number of specimens examined.